

# Annotated checklist of the Swiss bees (Hymenoptera, Apoidea, Anthophila): hotspots of diversity in the xeric inner Alpine valleys

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## Abstract

We present a checklist of the Swiss bees and provide information on the distribution of every bee species in all 26 Swiss cantons. 632 species are reported, including the European honeybee *Apis mellifera* Linnaeus, 1758 and the exotic species *Megachile sculpturalis* Smith, 1853. Species richness in each canton was correlated with the canton area, with the four largest cantons hosting the highest number of species. Bee diversity hotspots were located in some Alpine inner valleys characterized by a dry and warm climate due to the rain shadow effects of surrounding mountains. These hotspots are mostly located in the steppe-like habitats of the Valais and Graubünden cantons. They host diverse wild bee communities which include a unique assemblage of submediterranean faunal elements and subalpine species. In addition, these habitats host rare species with strongly disjunct distributions in Europe, further stressing the conservation priority of these habitats for wild bee conservation. Intensive faunistic surveys performed in the last 20 years have revealed that about 20 bee species, either previously unknown for Switzerland or which had disappeared from the country for several decades, have colonised areas close to the borders of France and Italy. Most of these new or reappeared species were observed in the warmest area of the country and presumably colonized or recolonized the country from neighbouring regions following global warming. Lastly, DNA barcodes are presented for 394 specimens, including for many species so far not represented in the BOLD database. The taxonomic status of numerous unclear taxa is briefly discussed based on combined genetic and morphological analyses.

## Key Words

Bees, pollinators, conservation, DNA barcoding, biodiversity, biogeography

## Introduction

Despite its small size, Switzerland has received much attention from entomologists for more than a century. This is particularly true for the Alps which cover nearly 60% of the country, and which have attracted botanists and entomologists for a long time, resulting in numerous studies documenting the Swiss flora and fauna (see for example Morawitz (1867) for an early work on Swiss Alpine bees).

The first author who extensively studied the Swiss bee fauna was Emil Frey-Gessner (1826–1917; Carl and Steck 1918). After being employed as a teacher near Aarau, Frey-Gessner was for some time the curator of the Hymenoptera collection of the Natural History Museum in Geneva. He collected in different places in Switzerland, mostly around Geneva, but also in the Valais, in Ticino, and in some localities in the Alps. He also identified bees from other Swiss entomologists, mostly Baptiste Jacob



(1830–1918; region of Neuchâtel), Henri Tournier (1834–1904; region of Geneva), Moritz Paul (1835–1898; region of Sierre, Valais), Walter Schmid (1843–1904; region of Basel), Emile Favre (1843–1905; region of Martigny and Sierre), and Theodor Steck (1857–1937; regions of Bern and Basel). Frey-Gessner compiled the first monograph of the Swiss bees, published as supplements to the *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* (Frey-Gessner 1899–1912). In this first treaty of the bees of Switzerland, 454 “species” and 52 “varieties” were recognized; translating these numbers into a precise count of species is difficult since these varieties include both colour morphs (e.g., *Bombus mucidus* var. *mollis* Pérez, 1879, the slightly lighter form of *B. mucidus* Gerstäcker, 1869) or valid species (e.g., *B. pomorum* var. *elegans* Seidl, 1837, the valid species now referred to as *B. mesomelas* Gerstäcker, 1869). The main part of his collection is preserved as a separate collection in the Natural History Museum of Bern; it is very well-preserved and still organized as Frey-Gessner originally arranged it, so that the records published in his monograph can be backed up with the precise specimens studied (see for example Blüthgen 1921). Frey-Gessner wrote locality information by hand on small labels (Suppl. material 1: fig. S1A); the date is only indicated as day and month; most specimens also bear a printed number, probably referring to a species catalogue; for some common localities, the locality is printed, the date (without year) being added by hand (Suppl. material 1: fig. S1A, B). His collection is remarkably well-maintained, with most specimens bearing locality labels; no apparently mislabeled specimens has been detected (but see comments under *Epeolus alpinus* Friese, 1893 for an obvious exception).

Jacques de Beaumont (1901–1985; see Besuchet 1986), a renowned sphecid wasp specialist, was the next important author who studied the Swiss bees, although his contributions on the bees were mostly a “by-product” of his intensive work on other groups of aculeate Hymenoptera, mostly the sphecid and pompilid wasps. De Beaumont, curator at the Museum of Zoology in Lausanne, collected bees in several regions of Switzerland, mostly western Switzerland, the Valais, Ticino, and the National Park region (Graubünden). He published three main accounts on the bees of Switzerland, two accounts on the bees of western Switzerland (de Beaumont 1955, 1960) and one account on the bees of the National Park region in the Graubünden (de Beaumont 1958). His well-preserved collection is mostly deposited at the Zoology Museum in Lausanne.

While de Beaumont and Frey-Gessner largely documented the wild bee fauna of western Switzerland, and to a very limited extent that of Ticino and of the National Park region in the Graubünden, large parts of Switzerland remained virtually uninvestigated until about 1960, especially the north-eastern corner, as well as Graubünden with the vast valleys of the upper Rhine river system. Even the eastern part of the Valais, corresponding to the German-speaking part of the Valais, perhaps the most

remarkable entomological “hotspot” in Switzerland due to its dry and continental climate, also remained largely unexplored until well after 1950. As noted by Amiet (1991), *Andrena probata* Warncke, 1973 and *A. ranunculorum* Morawitz, 1877 (Fig. 1), two remarkable and for the former, conspicuous and locally abundant species (at least historically), were only recorded in Switzerland after 1975, probably because they occur in the less accessible eastern part of the Valais, a region that Frey-Gessner and de Beaumont hardly visited.

The intensive work of Erwin Steinmann (1923–2020; see Müller 2021) has partly contributed to fill these gaps in the knowledge of the Swiss bee fauna, at least for the eastern part of the country (Graubünden). As a passionate mountain hiker, Erwin Steinmann investigated the Swiss Alpine bee fauna like no one else. He published an account on the bee fauna of the dry inner Alpine valleys (Steinmann 2002). His collection is preserved in the Natural History Museum of Chur, Graubünden.

The Swiss bee fauna is and will forever be associated with the name of Felix Amiet, who has dedicated much of his life to the study of the Swiss bees. Felix Amiet started his work on the bees in the 1960s. After that and until now, he has explored every corner of Switzerland to study its bees. He has assembled the most comprehensive collection to date, with well-preserved specimens from all biogeographic regions of the country. His collection is preserved in the Natural History Museum of Bern. Felix Amiet published the first checklist of the Swiss bees (Amiet 1991), where 575 species are mentioned; he then coordinated the publication of the six volumes of the atlases on the Swiss bees, which include distribution maps and identification keys for all species, and which were published in the series *Fauna Helvetica* (Amiet et al. 1999–2017). A first volume on the genus *Bombus* was published in the series *Insecta Helvetica* (Amiet 1996). The publication of these well-known identification keys has been the opportunity for him and his coauthors to entirely revise the museum specimens preserved in Swiss institutions, initiating the creation of the important database that underlies the present work. The activities of F. Amiet and E. Steinmann paved the way for numerous surveys of the native bee fauna, which were carried out from the 1980s onwards, predominantly as part of student theses and expert reports in different regions of Switzerland.

## Goal of the present checklist

The present checklist builds upon the previous work coordinated by Felix Amiet. Since 2012, much faunistic work has been conducted on the Swiss bees in a project aiming at updating the Red List of the Swiss bees; during this project, numerous inventories have been undertaken, partly in poorly investigated regions of Switzerland. Several new species for Switzerland have been found, and our knowledge of the distribution of the bees has substantially improved. In parallel, bee systematic studies have seen a





**Figure 1.** *Andrena probata* (left) and *Andrena ranunculorum* (right), two rare and emblematic species of the dry, inner Alpine Valleys of Switzerland. Pictures by Dimitri Bénon ([www.swisswildbees.ch](http://www.swisswildbees.ch)).

renewed impetus, in part due to the increased use of genetic markers to delineate species, leading to numerous taxonomic changes in the central European fauna. Before the publication of the Swiss red list (Müller and Praz, in press), we wish to summarize all these changes in the present work. We thus present a revised checklist of all Swiss bee species, giving for each species its distribution in all cantons of Switzerland. We also comment on each species: i. if it is new for Switzerland; ii. if it is a recently described species, or a recently recognized taxon previously treated as a synonym; iii. if its current distribution is different from that previously published (Amiet et al. 2001–2017), for example due to identification errors, to the finding of new populations, or to marked range expansions; iv. if the taxon is referred to differently in recently published bee checklists in Europe (Ghisbain et al. 2023; Scheuchl et al. 2023; Reverté et al. in press) and v. if there are open taxonomic questions that require additional work.

## Methods

### Critical examination of ancient records

As in other central or northern European countries, the bee fauna of Switzerland has seen massive declines, which gradually began after the main rivers had been channeled and the lowland areas subjected to urbanization and agricultural intensification. The few scientific collections that predate these important changes are thus irreplaceable testimonies of historical bee diversity. Unfortunately, these collections are small and their geographic coverage very fragmentary; moreover, the standards for curating specimens, especially with respect to the locality information on the labels, were not those of today. Consequently, some of these collections are somehow problematic, and some records dubious, for exam-

ple because the supposed locality information refers to the place of residence of the author, or simply because of labelling mistakes. We followed here the guidelines of Monnerat et al. (2015) to accept or reject records from such ancient collections. Briefly, a record is accepted if it originates from a “reliable” collection (see below), if a more or less accurate locality is indicated on the label, if this label is original (i.e., written by the collector and not recopied or added posteriorly; see Suppl. material 1: fig. S1), if the record is ecologically plausible (e.g., in term of phenology, habitat or, for cuckoo bees, the presence of the host), and if the record lies within the known potential or former distribution of the species in Europe.

Given the difficulties inherent in the identification of bees, we only validated records that are based on a preserved specimen; some old records based only on literature mentions are not validated (see for example the case of *Andrena hystrix* Schmiedeknecht, 1883, below). As indicated above, one criterion to validate or reject isolated records is whether the record lies within the overall distribution of the species in Europe (Monnerat et al. 2015), especially for species whose presence in Switzerland is based on a single specimen or a single collecting event. This criterion can prove challenging to evaluate given that the distribution of numerous bee species has drastically changed since the 19<sup>th</sup> century and given the poor knowledge of the historical distribution of numerous bee taxa in Europe (Tischendorf 2020). For example, *Andrena incisa* Eversmann, 1852, with numerous independent and reliable records in Switzerland between 1884 and 1939, is very rare in Europe, with ancient (<1970) records from Spain and Ukraine (as well as possibly Poland), and current records only from Turkey and Central Asia (T. Wood, pers. communication). To state that the records in Switzerland lie within the distribution of this bee in Europe would be a stretch, yet there are absolutely no doubts concerning these Swiss records. Similarly, numerous species



with reliable historical records near Geneva and no other record in central Europe, are entirely unknown in nearby parts of France, with confirmed records only in southern France, more than 200 km from the Swiss records (e.g., *Andrena mucida* Kriechbaumer, 1873, with confident records in the Geneva region; see below). Accepting or rejecting a historical record, especially if based on a single specimen, is thus to some extent an arbitrary process. As stressed above, the historical record of bees in Switzerland (and generally in central Europe) is extremely incomplete; compared to other groups (e.g., Coleoptera or Lepidoptera), bees are underrepresented in historical collections; in addition, bee communities are highly dynamic, and some rare species such as cuckoo bees, are difficult to detect. It is thus not surprising that the repeated sampling of bees in particularly rich habitats will continue to uncover regionally new species even after decades of sampling, and that such repeated sampling produces lists of species characterized by a high number of singletons.

In some insect groups, occurrences based on isolated individuals are sometimes considered to represent erratic individuals (vagrants) outside their reproductive range. Examples include historical records of butterflies in southern Switzerland, for example *Gonepteryx cleopatra* (Linnaeus, 1767) in Ticino or *Coenonympha dorus* (Esper, 1782) in the Geneva region; both species are not considered to be native in Switzerland and were not evaluated in the red list of the Swiss butterflies (Wermeille et al. 2014). We did not adopt this approach for the Swiss bees, for the following reasons. First, there is no indication that bees have a migratory behavior, unlike numerous species of butterflies. Second, as indicated above, singletons are a common feature of all bee surveys, simply because some species are particularly hard to detect. For these reasons, we consider each species observed at least once within Swiss territory as native and potentially reproducing, with the exception of the exotic species *Megachile sculpturalis* Smith, 1853 and one recent, isolated record of *Osmia latreillei* (Spinola, 1806) (see below).

Unlike in some other insect groups, notably the Coleoptera (Monnerat et al. 2015), most Swiss collections of Hymenoptera can be considered as reliable. Two problematic collections with respect to the bees are those of Henri Tournier (1834–1904; Suppl. material 1: fig. S1G) and Walter Schmid (1843–1904; Suppl. material 1: fig. S1F). Tournier collected numerous specimens near his home in Peney (Satigny, Geneva), a small village located 250 m from the shore of the Rhone River. At that time, the Rhone River was not channeled, and Tournier was probably able to collect in vast sandy habitats near his house. He also exchanged material with other entomologists. Several records of Tournier supposedly from Peney have been suggested to be erroneous (e.g., de Beaumont 1946; Neumeyer 2008; Neumeyer and Merz 2012; Neumeyer 2014). Based on the examination of his entire bee collection, the majority of us conclude that the bee collection is overall reliable and that most specimens labeled with “Peney” (usually only indicated by “P.” and the date; Suppl. material 1: fig.

S1G) were probably indeed collected near Peney. Another abbreviated locality is “R.” for “Reculet”, the highest peak of the Jura mountains, where Tournier collected an interesting series of bees, among other numerous specimens of *Bombus mendax* Gerstäcker, 1869, a species now extinct in the Jura. At Tournier’s time, many species were not yet described, especially in difficult species groups (e.g., *Andrena*, *Lasioglossum*, *Nomada*), and the knowledge of the bees in central Europe was very fragmentary, since the major catalogues and identification works (e.g., Dalla Torre 1896; Friese 1895–1901; Schmiedeknecht 1907) were not yet published. Despite this, the bees preserved in the Tournier collection, and labeled as being from Peney, do in fact belong to central European species, with only a few exceptions that are possibly based on mislabeled specimens (see below). As an illustration, we identified the numerous specimens of the subgenus *Micrandrena* of the Tournier collection, superficially very similar species that no one could identify at Tournier’s time. All *Micrandrena* specimens belong to species currently present near Geneva, or to species also collected by Frey-Gessner near Geneva at the same time as Tournier (*Andrena distinguenda* Schenck, 1871, *A. floricola* Eversmann, 1852, *A. niveata* Friese, 1887, *A. pauxilla* Stöckert, 1935, and *A. pusilla* Pérez, 1903). The same is true for the species of the taxonomically challenging subgenus *Taeniandrena*. Nevertheless, some records represented by singletons in Tournier’s collection belong to species whose known distribution area does not encompass Switzerland. These records are possibly based on mislabeled specimens, and the records for three species are not accepted here (*Andrena ventricosa* Dours, 1873, *Lasioglossum sphecodimorphum* (Vachal, 1892) and *Colletes nasutus* Smith, 1853), following Monnerat et al. (2015). These cases are briefly discussed below.

The collection of Walter Schmid is slightly more problematic because the specimens were not labeled with original locality data by Schmid himself. All specimens in his collection bear a printed label that simply mentions “Basel, W. Schmid” (Suppl. material 1: fig. S1F), and it is probable that these labels were added after W. Schmid’s death. Consequently, some of Schmid’s records supposedly from Basel are probably erroneous (see for example *Nomada gribodoi* Schmiedeknecht, 1882, below); moreover, some records may originate from the much larger Basel region (including nearby France or Germany) and not from the Swiss Basel region. However, Frey-Gessner corresponded with W. Schmid and confirmed in his book some unique records for Switzerland, such as *Andrena sericata* Imhoff, 1868, *Colletes collaris* Dours, 1872 and *Systropha planidens* Giraud, 1861, all three of which occur north of Basel in the Rhine Valley, and which W. Schmid collected near Basel according to Frey-Gessner. We consider the historical presence of these species highly likely in the Basel region. Consequently, to simply discard all of W. Schmid records would be erroneous, and for this problematic collection we accepted occurrences that are plausible from a biogeographic point of view and that are backed up with a specific reference in Frey-Gessner’s book.



## The Swiss bee dataset

All Swiss bee records, including those based on museum material, faunistic inventories or citizen-science based observations, are assembled into a database centralized at info fauna, Neuchatel ([www.infofauna.ch](http://www.infofauna.ch)). The main task of info fauna is to maintain faunistic databases, to publish them as open resource at a low resolution ( $5 \times 5$  km) nationally and internationally, and to diffuse precise occurrence data to actors active in conservation, such as nature reserve managers and conservation agencies. The entire bee dataset can be accessed freely on GBIF (Praz et al. 2022), although in this open-access dataset the coordinates are rounded to a grid of  $5 \times 5$  km; the underlying reason is that numerous occurrences are private, and for these private occurrences, the observer maintains exclusive ownership of the precise data. Distribution maps with a precision of  $5 \times 5$  km can be accessed freely at <https://lepus.infofauna.ch> and the biology of the Swiss species is summarized in a dedicated website (<https://species.infofauna.ch/groupe/1>).

## Subspecies

Subspecies are not recognized in this dataset. In some cases, the initial database assembled for the publication of the identification keys by Amiet et al. (1999–2017) included subspecies. Overall, the recognition of subspecies is a controversial matter in systematics; it may make sense in some cases, for example to highlight incipient speciation, or for pragmatic, conservation purposes for geographically isolated units that may eventually be treated as a distinct taxon. However, the subspecies rank has also been used in the past for distinct colour morphs co-occurring in sympatry with regular-looking forms (e.g., the numerous forms within *Bombus humilis* Illiger, 1806, or *Bombus confusus* Schenck, 1859 and *Bombus confusus* “*paradoxus*” Dalla Torre, 1882), an approach that makes little sense since such forms do not represent significant evolutionary or conservation units. Overall, subspecies are not recognized in legal documents or by local conservation practitioners in Switzerland, and for such a small country, we see little need to recognize subspecies for bees. In some species, the Swiss populations belong to a recognized subspecies that is distinct from the nominal subspecies. An example in *Lasioglossum limbellum* (Morawitz, 1876): the nominal subspecies *L. limbellum limbellum* occurs eastwards from the Pannonian region of Austria, while the subspecies *L. limbellum ventrale* (Pérez, 1903) occurs westwards, including in Switzerland (Ebmer 1988). For practical reasons, we do not mention the subspecies in such cases (the subspecies are mentioned in Amiet et al. 2001–2017). We discuss below how we treat previously recognized subspecies (see for example under *Halictus confusus* Smith, 1853, *Nomada panzeri* Lepelletier, 1841, *Panurginus montanus* Giraud, 1861 and *P. sericatus* (Warncke, 1972)).

## Species aggregates

In bees, there are numerous groups of species where a confident identification is only possible in fresh specimens or when some specific characters are visible, for example the male genitalia. In addition, only one sex can be identified with confidence in several groups. For example, the females of the *Halictus simplex* group (*Halictus simplex* Blüthgen, 1923, *H. langobardicus* Blüthgen, 1944 and *H. eurygnathus* Blüthgen, 1931) are nearly impossible to separate (Ebmer 1969; Amiet et al. 2001; Pauly 2015; pers. obs.). In such cases, all females were lumped in a species aggregate and the distribution data is inferred based on male specimens only. The different aggregates recognized in the Swiss database are listed in Table 1. For some difficult groups (e.g., the *Bombus terrestris*-group or the *Hylaeus gibbus*-group), an identification at the species level was only performed in typical specimens where a set of different morphological characters was in agreement. If one important morphological character was equivocal, the specimen was identified at the aggregate level.

## Generic classification

We adopt here the classification of Michener (2007) with a few exceptions, which are detailed here. Compared to previous work on the Swiss bees (Amiet et al. 2001–2017) this new classification leads to the break-up of the genus *Anthophora* into *Anthophora* and *Amegilla*, of the non-parasitic Anthidiini into the six genera *Anthidiellum*, *Anthidium*, *Icteranthidium*, *Pseudoanthidium*, *Rhodanthidium* and *Trachusa*, of the genus *Osmia* into *Osmia*, *Hoplitis* and *Protosmia*, of the genus *Dioxys* into the genera *Allodioxys* and *Dioxys*, and of the genus *Epeolus* into the genera *Epeolus* and *Triepeolus*. In contrast to Michener (2007), the genus *Nomiapis* is recognized for the species *Nomiapis diversipes* (Latreille, 1806) (formerly *Nomia diversipes* or *Pseudapis diversipes*), following Pauly (1990), Baker (2002), Astafurova and Pesenko (2006), Bossert et al. 2021 and Wood and Le Divelec (2022). Then, the genera *Coelioxys* and *Dioxys* are considered to be masculine (Rasmont et al. 2017). In the tribe Eucerini, several changes have recently been proposed (Dorchin et al. 2018; Freitas et al. 2023; Dorchin 2023), which result in the recognition of only two genera for the central European fauna, *Eucera* and *Tetralonia*, in contrast with the classification of Michener (2007) which recognized the genus *Tetraloniella* in addition to *Tetralonia*. The genus *Eucera* includes all two-celled species plus the three-celled subgenus *Synhalonia*, while the genus *Tetralonia* includes all other three-celled species, including species formally included in the genus *Tetraloniella*. Consequently, the three-celled species *Eucera* (*Synhalonia*) *hungarica* Friese, 1896 is treated here as a member of *Eucera*, not of *Tetralonia* as in Amiet et al. (2007). Lastly, we treat *Seladonia* as a subgenus of *Halictus* and not as a distinct genus, following Ebmer (1988), Michener (2007), Gibbs et al. (2012), Scheuchl and Willner (2016), and Scheuchl et al. (2023).



**Table 1.** The species aggregates recognized in the Swiss bee database.

Species aggregate	Included species	Remark
<i>Lasioglossum alpigenum/bavaricum</i> aggr.	<i>Lasioglossum alpigenum</i> , <i>L. bavaricum</i>	All females of these two species are included in this species aggregate, unless a DNA-based identification was performed.
<i>Lasioglossum fratellum/subfulvicorne</i> aggr.	<i>Lasioglossum fratellum</i> , <i>L. subfulvicorne</i>	All females of these two species are included in this species aggregate.
<i>Hylaeus gibbus</i> aggr.	<i>Hylaeus confusus</i> , <i>H. gibbus</i> , <i>H. incongruus</i>	Most specimens were identified using morphology; specimens that could not be re-examined recently, as well as morphologically unclear specimens, were included in this aggregate.
<i>Panurginus montanus</i> aggr.	<i>Panurginus montanus</i> , <i>P. sericatus</i>	Most females of these two species were included in this aggregate.
<i>Andrena proxima</i> aggr.	<i>Andrena alutacea</i> , <i>A. ampla</i> , <i>A. proxima</i>	Morphologically unclear specimens (mostly males, but also worn females) were included in this aggregate. All specimens from the Valais upstream from Martigny were assigned to <i>A. ampla</i> (McLaughlin et al. 2023).
<i>Halictus simplex</i> aggr.	<i>Halictus eurygnathus</i> , <i>H. langobardicus</i> , <i>H. simplex</i>	All females of these three species are included in this species aggregate, unless a DNA-based identification was performed.
<i>Hylaeus taeniolatus/pictipes</i> aggr.	<i>Hylaeus pictipes</i> , <i>H. taniolatus</i>	Females were systematically assigned to this aggregate until 2019; thereafter, most females were separated based on their morphology.
<i>Bombus terrestris</i> aggr.	<i>Bombus cryptarum</i> , <i>B. lucorum</i> , <i>B. magnus</i> , <i>B. terrestris</i>	All workers were included in this species aggregate, unless identified using DNA. Queens and males were mostly identified to the species level.

DNA barcoding

For the present work, numerous identifications have been verified using DNA barcoding, following lab protocols published elsewhere (e.g., Praz et al. 2019). Our general approach is to amplify the entire or part of the 658-bp “barcoding” fragment of the mitochondrial gene Cytochrome Oxidase I in two independent PCRs (Polymerase Chain Reactions) with the primers pairs LepF/LepR and UAE3/LepR (Suppl. material 2), producing fragments of 658 and 409 bp, respectively. These two PCRs can be done together with identical PCR conditions (see Praz et al. 2019, 2022). The PCR products were examined on an agarose gel; if both PCR worked, the 658-bp fragment was sequenced using the reverse primer LepR, and the 409-bp fragment with the forward primer UAE3; both sequences were assembled in Geneious Prime 2022.2.2, yielding the complete 658-bp fragment. For old specimens (> 10 years), often only the 409-bp fragment was successfully amplified, and this fragment was then sequenced bidirectionally with the primers UAE3 and LepR. The advantage of using two independent PCRs is that without increasing sequencing costs, the technique provides a way of checking for contamination or pipetting errors, as well as a way of minimizing the sequencing of nuclear pseudogenes (NUMTs). In addition, approximately 10% of the sequences produced with the primer pairs LepF/LepR in bees amplify *Wolbachia* DNA; this ratio was much lower with the primers UAE3/LepR. For some groups that failed to produce clear chromatograms with the primers LepF, LepR and UAE3, clade specific primers were developed; if neither the 658-bp nor the 409-bp fragments yielded clear chromatograms, these specific primers were used. A list of all primers used is given in Suppl. material 2.

We generated DNA barcodes with the following aims. First, in numerous cases, DNA-assisted identifications allowed to delineate the distribution of some species and generated confidently identified material to evaluate

morphological criteria (see for example the case of the *Hylaeus gibbus*-group, below). Second, we generated DNA barcodes to evaluate the taxonomic status of some “forms” with unclear taxonomy. Lastly, we generated DNA barcodes for Swiss species not yet represented in DNA barcode libraries ([www.bold.org](http://www.bold.org), hereafter BOLD). All generated DNA barcodes have been submitted to BOLD; a full list of specimens for which DNA barcodes were generated, including locality information as well as BOLD accession numbers, is given in Suppl. material 3. In all figures, new sequences are indicated in red; all other sequences have been downloaded from the BOLD website.

Results

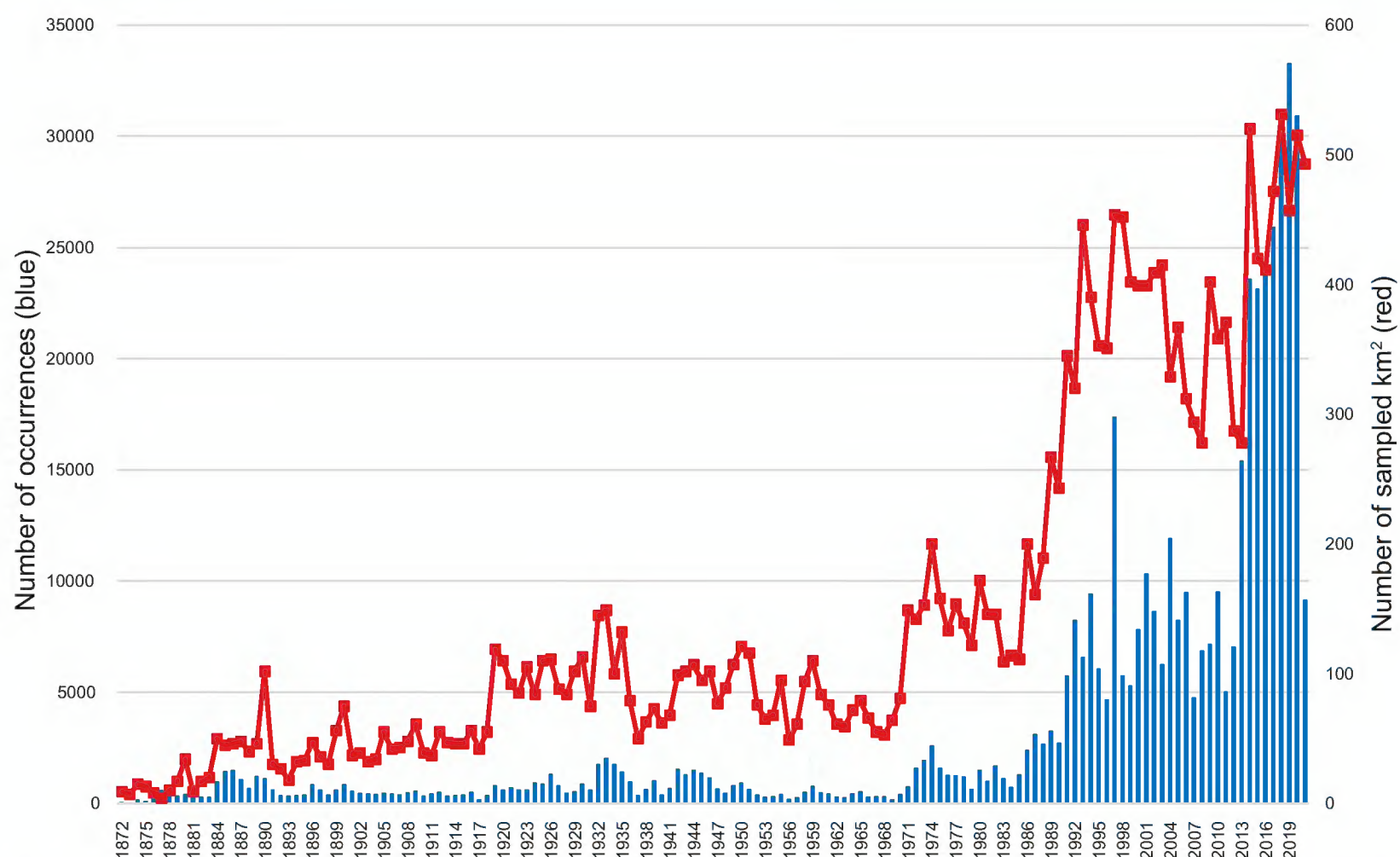
The Swiss bee checklist

The database includes 473653 occurrences between 1817 and 2021 (inclusive), distributed in 7027 1 × 1-km grid cells; all records, even the historical records, are attributed to one 1 × 1-km grid cell, corresponding to the kilometer grid of the national topographic maps ([www.map.geo.admin.ch](http://www.map.geo.admin.ch)); one occurrence may include several specimens when more than one specimen was collected at the exact same locality on the same day. The evolution of the database in time is shown in Fig. 2.

To date, 632 bee species have been recorded for Switzerland, including one exotic species, *Megachile sculpturalis* and the European honeybee, *Apis mellifera* Linnaeus, 1758. The distribution of these species in all Swiss cantons is given in Table 2 and Suppl. material 4.

A distance-based tree was build using the unweighted pair group method with arithmetic mean (UPGMA) with all newly produced sequences (Suppl. material 5). In this tree, only sequences above 300 bp were included; previously published DNA barcodes from Swiss studies were also included (Praz et al. 2019, 2022; Gueuning et al. 2020; McLaughlin et al. 2023).





**Figure 2.** Evolution of the Swiss bee database over time, showing the number of occurrences (blue) and the number of sampled  $1 \times 1$  km-quadrates (number of quadrates with at least one bee observation).

## Comments on selected species

### *Amegilla salviae* (Morawitz, 1876)

This species is known from a single specimen collected in Sierre by Frey-Gessner. Sierre is a famous entomological locality; it lies in the Rhone Valley in the Valais and the region between Sierre and Leuk (the alluvial site of Finges) was until the beginning of the 20<sup>th</sup> century the last place in the Valais where the Rhone River was not channeled. Since Frey-Gessner's collection is reliable, this record is accepted, even if it represents an isolated record at the European scale. That such a conspicuous species was collected only once is surprising, but illustrates how even the Valais fauna was poorly sampled until well into the 20<sup>th</sup> century (see also comments under *Nomada confinis* Schmiedeknecht, 1882 and *Tetralonia pollinosa* (Lepeletier, 1841)). Frey-Gessner was one of the last entomologists who could visit the alluvial site of Finges before the construction of the Susten water dam in 1910. The construction of this dam for electricity production likely led to the loss of the natural river dynamic and to important habitat degradation at this site.

### *Andrena afzeliella* (Kirby, 1802)

This species has recently been separated from *A. ovatula* (Kirby, 1802), a taxon which has so far not been reported from Switzerland (Praz et al. 2022). The closest record of *A. ovatula sensu stricto* known to us is a male collected near Freiburg in Breisgau (Flughafen, Mull, 22.4.1992, leg. & coll. C. Schmid-Egger, *A. ovatula* s. str. det. F. Burger 2001, confirmed C. Praz 2022), only 50–60 km north of Basel, rendering the presence of *A. ovatula* in

Switzerland possible, at least in the past, for example in the region of Basel. A morphological separation of *A. afzeliella* and *A. ovatula* is mostly possible, at least in the female sex (see identification key in Praz et al. 2022).

### *Andrena alfkenella* Perkins, 1914

Males of this taxon have so far often been misidentified in Switzerland, mainly with *A. floricola* and *A. minutula* (Kirby, 1802). All three species exhibit distinct DNA barcodes (Suppl. material 5) and can readily be identified in the female sex. We barcoded several male specimens initially identified as *A. alfkenella* or *A. floricola*, which highlighted the fact that the males of *A. alfkenella* have mostly been misidentified as *A. floricola*, and the males so far identified as *A. alfkenella* mostly belong to *A. minutula*. Unlike the indication in Amiet et al. (2010), the male of *A. alfkenella* has the terga shiny and the stigma at least partly yellow-brown, as in *A. floricola*, from which it differs by the more sparsely punctate terga (comparison with reference material is needed and some specimens are difficult to identify) (see also Schmid-Egger and Scheuchl 1997 and Wood 2023a). See additional comments under *A. floricola*.

### *Andrena allosa* Warncke, 1975

The status of this species and its distribution in Europe were presented by Praz et al. (2019). This western Alpine species reaches its eastern limit in the Bernese Alps near Kandersteg. Although it has never been found in the Swiss Jura, an observation on the Salève south of Geneva (France) renders its occurrence in the Western Jura possible. *Andrena allosa* is included in the identification key given in Praz et al. (2019).



**Table 2.** Checklist of the Swiss bees, showing the presence of each species in each canton. Open circles indicate records before 2000, closed circles after 1999. Abbreviations: AG: Aargau; AI: Appenzell Innerrhoden; AR: Appenzell Ausserrhoden; BE: Bern; BL: Basel-Landschaft; BS: Basel-Stadt; FR: Fribourg; GE: Geneva; GL: Glarus; GR: Graubünden; JU: Jura; LU: Luzern; NE: Neuchâtel; NW: Nidwalden; OW: Obwalden; SG: St. Gallen; SH: Schaffhausen; SO: Solothurn; SZ: Schwyz; TG: Thurgau; TI: Ticino; UR: Uri; VD: Vaud; VS: Valais; ZG: Zug. This table is also available as a supplemental table (Suppl. material 4).

Species	AG	AI	AR	BE	BL	BS	FR	GE	GL	GR	JU	LU	NE	NW	OW	SG	SH	SO	SZ	TG	TI	UR	VD	VS	ZG	ZH	Number of Cantons	Number of Cantons (after 2000)
Aglaopis tridentata					●			●		●	●												○		●		6	5
Amegilla albigena									○															●	●		2	1
Amegilla garrula								○		●											●				○		4	2
Amegilla quadrifasciata						○			○															○	○		3	0
Amegilla salviae																								○	○		1	0
Ammobates punctatus																								●		1	1	
Andrena aeneiventris								●		○											●		○		●		5	3
Andrena afrensis																								●		1	1	
Andrena afzeiella	●			●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	24	24
Andrena agiissima				●	●	○	○	●		●			●			●	●	○			●		●	○	○	●	13	9
Andrena alfenella	●			●	●	○	●	●		●	●	●	○				●				●		●	●	●	●	16	14
Andrena allosa				●			●									●							●	●	●		6	6
Andrena alutacea							○			●			●			○					●					●	7	5
Andrena amieti				●			●		●	●			●			●	●				●		●		●		11	11
Andrena ampla										●											●				●		3	3
Andrena apicata	○		●	●	●		●			●	●	●	●	●	●	●	●	●	●	●	●	○	●	●	●	○	17	14
Andrena argentata				○				○		○											●		○		○		6	1
Andrena assimilis				○																				○	○		2	0
Andrena barbareae										●						●					●				●		5	4
Andrena barbilabris	●			●	●	○	●	○		●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	21	19
Andrena bicolor	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	25	25
Andrena bimaculata				○				○		●											●		●	●	●		6	4
Andrena bucephala	●		●	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	●		●	●	●	●	18	18
Andrena chrysopus																				●				●		2	2	
Andrena chrysosceles	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	26	26
Andrena cineraria	●	●	●	●	●	●	●	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	26	25
Andrena clarkella				●	●	○	●			●	●	●	●	●	●	●	●	●	●	●	●	○	●	●	●	●	16	14
Andrena coitana				○		○	●	○	●	●			○			●					●		●	●	●		11	7
Andrena combinata	●			●			○	○		●	●	●	●	●		○	●	●	●	●	●	●	●	●	●	●	19	16
Andrena confinis				○			○	●		●			○			○	○	○			●		○			○	10	3
Andrena congruens				○				○		●			○					○			●		●	●	●		9	4
Andrena curvungula			●	●			●	●		●	●		●				●	●	●				●	●	●	●	15	15
Andrena decipiens								○															○			3	0	
Andrena denticulata					●			○	●	●			○								●				○		7	5
Andrena distinguenda	●					○		○									●									4	2	
Andrena dorsata	●			●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	23	23
Andrena falsifica	●		●	●	●		○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	24	23
Andrena ferox				○				○		●			○								○			○	●		7	2



Species	AG	AI	AR	BE	BL	BS	FR	GE	GL	GR	JU	LU	NE	NW	OW	SG	SH	SO	SZ	TG	TI	UR	VD	VS	ZG	ZH	Number of Cantons (after 2000)
Andrena flavilabris								○																			1
Andrena flavipes	●			●	●	●	●	●	○	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	22
Andrena florea	●			●	●	●	●	●					●				●	●	●		●		●	●		●	13
Andrena floricola						○		○		○			○				○			○			○				8
Andrena florivaga											●																1
Andrena freygessneri							●			●											○						4
Andrena fucata	●	●	●	●		●	●	○	●	●	●	●	●	○		●	●	●	●	●	●	●	●	●	●	●	23
Andrena fulva	●			●		●	●	●		●	●	●	●	●		○	○	●	●	●	●		●	●		●	20
Andrena fulvago	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	26
Andrena fulvata	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	25
Andrena fulvicornis	●				●						●					●	●	●	●	●							4
Andrena fulvida				●			○			●						●					●						5
Andrena fuscipes							●	○		●											●						4
Andrena fuscosa																					●						3
Andrena gelrae							○	●										○									1
Andrena gravida	●		●	●	●	●	●	●		●	●	●	●	●	●			○	●	●		●	●	●	●	●	7
Andrena haemorrhoa	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●		●	●	●	●	●	22
Andrena hattorfiana	●		●	●	●	○	●	●	●	●	●	●	●	○		●	●	●	●	●	●	●	●	●	●	●	26
Andrena helvola	●		●	●	●	●	●	●	●	●	●	●	●	●		●	●	●	●	●	●	○	●	●	●	●	25
Andrena hesperia				●	●					●	●	●	●	●				○		●		●					23
Andrena humilis	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	3
Andrena hypopolia								○																			26
Andrena incisa																								○			2
Andrena intermedia		●	●	●		○	●	○	●	●	●	●	●	●	●		○		●	●		●	●	●		●	2
Andrena labialis				●	●	●		●	●	●			●		●		○	●	●		●		●	●			20
Andrena labiata	●	●	●	●	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●		●	●	●	●	●	13
Andrena lagopus	●			●	●	●	●	●		●	●	●	●			○	●	●	●	●	●	●	●	●	●	●	25
Andrena lapponica	●			●		●	○	●	●	●	●	●	●	●				●		●	●	●	●	●	●	●	17
Andrena lathyri	●			●	●	●	○	●		●	●	●	●			●	●			●	●	●	●	●	●	●	15
Andrena lepida								○		●	●	●	●					●		●	●	●	●				20
Andrena limata	○			○		○		○		●											●		○				1
Andrena livens																					●						7
Andrena marginata	●			●			●	○		●						●				○	●		○	●	●	●	10
Andrena minutula	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	25
Andrena minutuloides	●			●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	23
Andrena mitis	●			●		●	●	●		●	●	●	●			●	●	●		●		●	●	●	●	●	17
Andrena montana				●			●		●	●												●					5
Andrena mucida				○	○			○		●		○	●								○		○	●			2
Andrena nana	●					○	●	●		●			●			●	●	●		●	○		●		●	●	17
Andrena nanula										●											●						2
Andrena nigroaenea	●			●		●	●	●		●	●	●	●	●	○			●	○		●	●	●	●	○	○	21
Andrena nigrolivacea	●			●	●	●					●		●			●		●					●	●		●	9
Andrena nigrospina						○		○			●		●					●					○				3



Species	AG	AI	AR	BE	BL	BS	FR	GE	GL	GR	JU	LU	NE	NW	OW	SG	SH	SO	SZ	TG	TI	UR	VD	VS	ZG	ZH	Number of Cantons Cantons	Number of Cantons (after 2000)
<i>Andrena nitida</i>	•		•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	25	25
<i>Andrena nitidiuscula</i>	•			•	•	•	•	•		•	•		•				•	•	•	•	•	•	•	•	•	•	17	15
<i>Andrena niveata</i>							•	•										•			•			•			5	2
<i>Andrena nuptialis</i>				•				•																•			2	1
<i>Andrena nychthemera</i>	•			•		•		•					•						•					•		•	6	0
<i>Andrena ovata</i>								•													•			•			2	1
<i>Andrena pallitarsis</i>						•		•		•											•						5	1
<i>Andrena pandellei</i>	•			•	•	•	•	•		•	•	•					•	•	•	•	•		•	•	•	•	17	17
<i>Andrena parviceps</i>							•	•															•		•		4	2
<i>Andrena pauxilla</i>								•																•			1	0
<i>Andrena pellucens</i>																					•						1	1
<i>Andrena pilipes</i>				•		•		•		•											•		•				8	1
<i>Andrena polita</i>				•						•							•		•		•		•	•		•	7	6
<i>Andrena potentillae</i>				•		•		•															•				6	3
<i>Andrena praecox</i>	•			•	•	•	•	•		•	•	•	•	•			•	•	•	•	•		•	•	•	•	22	21
<i>Andrena probata</i>							•	•		•														•			2	1
<i>Andrena propinqua</i>				•		•	•	•		•			•								•		•	•	•	•	10	5
<i>Andrena proxima</i>	•			•	•	•	•	•		•	•	•	•	•			•	•	•	•	•	•	•	•	•	•	22	21
<i>Andrena pusilla</i>						•		•													•		•				4	1
<i>Andrena ranunculorum</i>																							•				1	1
<i>Andrena rhenana</i>					•	•		•																			3	3
<i>Andrena rogenhoferi</i>				•	•		•		•	•			•	•			•		•		•		•				12	12
<i>Andrena rosae</i>	•			•	•	•	•	•		•	•	•	•	•			•	•	•	•	•		•	•	•	•	20	16
<i>Andrena ruficrus</i>	•			•			•			•			•	•					•		•		•	•	•	•	14	14
<i>Andrena rufizona</i>				•				•		•							•				•		•	•		•	8	4
<i>Andrena rufula</i>				•							•								•				•			•	6	6
<i>Andrena rugulosa</i>				•								•					•		•						•	•	6	4
<i>Andrena russula</i>				•			•	•		•			•					•			•		•		•	•	12	8
<i>Andrena saxonica</i>										•																	1	1
<i>Andrena schencki</i>	•			•	•	•		•		•	•	•	•	•			•	•	•	•	•		•	•			15	11
<i>Andrena scotica</i>	•	•		•	•	•	•	•	•	•	•	•	•	•			•	•	•	•	•		•	•	•	•	25	25
<i>Andrena semilaevis</i>				•		•	•	•		•	•	•	•						•		•		•	•	•	•	16	13
<i>Andrena sericata</i>						•																		•			2	0
<i>Andrena similima</i>										•											•						3	2
<i>Andrena simontomyella</i>								•													•						2	2
<i>Andrena strohmei</i>	•		•	•	•	•	•	•	•	•	•	•	•	•			•	•	•	•	•		•	•	•	•	24	24
<i>Andrena subopaca</i>	•		•	•	•	•	•	•	•	•	•	•	•	•			•	•	•	•	•		•	•	•	•	26	25
<i>Andrena suerimensis</i>								•																•			2	1
<i>Andrena symphyti</i>							•						•								•						2	1
<i>Andrena synadelpha</i>				•				•					•										•			•	7	3
<i>Andrena taraxaci</i>				•						•											•						2	2
<i>Andrena tarsata</i>				•		•			•	•			•								•		•	•			10	8
<i>Andrena tenuistriata</i>						•		•		•			•								•						1	1



Species	AG	AI	AR	BE	BL	BS	FR	GE	GL	GR	JU	LU	NE	NW	OW	SG	SH	SO	SZ	TG	TI	UR	VD	VS	ZG	ZH	Number of Cantons (after 2000)
<i>Andrena thoracica</i>						○				●											●			●			4
<i>Andrena tibialis</i>	●			●	●	●	●	●		●	●	●	●				●	●	●		●		●	●	●	●	19
<i>Andrena tridentata</i>									○																		1
<i>Andrena trimmerana</i>	●			●		○	○	●		●	●		●				●	○	○		●		●	●	●	●	15
<i>Andrena tscheki</i>																					○						1
<i>Andrena vaga</i>	●			●	●	●	●	●		●	●	●	●				●	●	●	●	●	●	●	●	●	●	21
<i>Andrena varians</i>	○			○		○		○		○			○					○			○		○	○		●	12
<i>Andrena ventralis</i>	●			●		●	●	●		●	●	●	●	○			●	●	●	●	●	●	●	●	●	●	21
<i>Andrena viridescens</i>	●		●	●	●	●	●	●	●	●	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	25
<i>Andrena vulpecula</i>										●											●						2
<i>Andrena wilkella</i>	●	●		●	●	●	●	●	●	●	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	24
<i>Anthidium strigatum</i>	●		●	●	●	○	●	●	●	●	●	●	●	●			●	●	●	●	●	●	●	●	●	●	24
<i>Anthidium cingulatum</i>				○		○		●		○			○												○		6
<i>Anthidium florentinum</i>										●											●						2
<i>Anthidium loti</i>								○													●						2
<i>Anthidium manicatum</i>	●			●	●	●	●	●	○	●	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	23
<i>Anthidium montanum</i>		●		●			●		●	●		●	●	●				○	●		●	●	●	●			16
<i>Anthidium oblongatum</i>	●			●	●	●	●	●		●	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	23
<i>Anthidium punctatum</i>	●			●	●	●	●	●	●	●	●	●	●	●	●		●	●	●	●	●		●	●	●	●	21
<i>Anthidium septemspinosum</i>						●				●			●								●						3
<i>Anthophora aestivalis</i>	●			●	●	○	●	●		●	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	21
<i>Anthophora balneorum</i>									○	○													○				3
<i>Anthophora bimaculata</i>								○		●											●						4
<i>Anthophora canescens</i>								○																			1
<i>Anthophora crassipes</i>										○																	2
<i>Anthophora crinipes</i>				●			●	●		●		○							●		●		●				10
<i>Anthophora dispar</i>																					●						1
<i>Anthophora fulvitaris</i>								○																○			2
<i>Anthophora furcata</i>	●			●	●	○	●	●	●	●	●	●	●	●			●	●	●	●	●	●	●	●	●	●	23
<i>Anthophora mucida</i>																					○						2
<i>Anthophora plagiata</i>				●		○		○		●			○									●					7
<i>Anthophora plumipes</i>	●		○	●	●	●	●	●	●	●	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	25
<i>Anthophora pubescens</i>								○		●											●						5
<i>Anthophora quadrimaculata</i>	●			●	●	●	●	●	●	●	○		●	●	●		●	●	●	●	●	●	●	●	●	●	22
<i>Anthophora retusa</i>										●											●						4
<i>Apis mellifera</i>	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	26
<i>Biastes emarginatus</i>								○																			3
<i>Biastes truncatus</i>										●														●	○		2
<i>Bombus alpinus</i>				●						●						○								●			7
<i>Bombus argillaceus</i>										●																	3
<i>Bombus barbutellus</i>	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	26
<i>Bombus bohemicus</i>	●	●	●	●	●	●	●	○	●	●	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	26
<i>Bombus campestris</i>	●			●	●	●	●	●	●	●	●	●	●	●			●	●	●	●	●	●	●	●	●	●	23



Species	AG	AI	AR	BE	BL	BS	FR	GE	GL	GR	JU	LU	NE	NW	OW	SG	SH	SO	SZ	TG	TI	UR	VD	VS	ZG	ZH	Number of Cantons	Number of Cantons (after 2000)
Bombus confusus				○			○	○		●			○	○	○						○	○	○	○	○	○	12	1
Bombus cryptarum				●					○	●	○		●	○	○	●			●	●		●	●	●	●		12	9
Bombus distinguendus				○				○					○										●				4	1
Bombus flavidus				●						●				●	●	○						○	●	●	●		9	7
Bombus gerstaeckeri		●		●			●		●	●		●		●	●	●			●	●		●	●	●	●		14	14
Bombus hortorum	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	26	26
Bombus humilis	●			●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	24	24
Bombus hypnorum	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	26	26
Bombus inexpectatus										●																3	3	
Bombus jonellus		●		●					●	●		●	●	●	●	●	●	○		●	●	●	●	●	●	●	16	15
Bombus lapidarius	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	26	26
Bombus lucorum	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	26	26
Bombus magnus													○													1	0	
Bombus mendax		●		●			●		●	●		●	○	●	●	●			●	●		●	●				15	14
Bombus mesomelas			○	●			●		●	●			●	○		●		○		●	●	●	●	●	●		16	12
Bombus monticola		●		●			●	○	●	●	●	●		●	●	●			●	●	●	●	●	●	●		15	14
Bombus mucidus		●		●			●	○	●	●	●	●	○	●	●	●			●	●	●	●	●	●			16	14
Bombus muscorum	●			○		○	●	○		●		●		○		●	○		○	●	●	●	●	●	●	●	16	9
Bombus norvegicus			●	●	●		●	●	●	●	●	●	●		○	●	●	●	●	●	●	●	●	●	●	●	22	21
Bombus pascuorum	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	26	26
Bombus pomorum	○			○	○	○	○	○		○	○	○	○					○		○		○	○	○	○	○	16	0
Bombus pratorum	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	26	26
Bombus pyrenaeus		●		●			●		●	●		●		●	○	●			●	●		●	●				14	13
Bombus quadricolor		●		●			●	○	●	●	○	○	○	○	○	●			○		●	●	●	●	○	○	18	10
Bombus ruderarius	●	●	○	●	●		●	●	●	●	●	●	●	●	●	●	●	●	●	○	●	●	●	●	●	●	24	22
Bombus ruderatus	●	●		●		○	●	●	●	●	●	●	●			●	●	●	●	●		●	●	●	●	●	18	17
Bombus rupestris	●	●	○	●	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	25	24
Bombus sichelii		○	○	●			●		●	●		●	○	●	●	●			○		●	●	●				17	13
Bombus soroensis	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	26	26
Bombus subterraneus	●	●		●	●		○	○		●	●	●	●			○	●	●	●	●			●	●	●	●	19	16
Bombus sylvorum	●	●		●	●	●	●	●		●	●	●	●	○		●	●	●	●	●	○	●	●	●	●	●	23	21
Bombus sylvestris	●	●	●	●	●	●	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	26	25
Bombus terrestris	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	24	24
Bombus vestalis	●			●	●	●	●	●	●	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	22	22
Bombus veteranus	●	●	○	●			○	○			●	●	●	○		●	○	●	●	○			●	●		●	18	11
Bombus wurflenii	●	●	●	●	●		●	○	●	●	●	●	●	●	●	●	●	●	●	○	●	●	●	●	●	●	24	22
Ceratina chalcites																										1	1	
Ceratina chalybea	●			●	●	○	●	●	●	●	●		○					●			●	●		●			13	11
Ceratina cucurbitina	●			●	●	●	●	●		●	●		●				●	●	●		●	●	●	●	●	●	15	15
Ceratina cyanea	●		○	●	●	●	●	●	●	●	●	●	●				●	●	●	●	●	●	●	●	●	●	24	23
Ceratina gravidula										●															○		3	2
Ceratina nigrolabiata																					●						1	1
Chelostoma campanularum	●		●	●	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	24	24



Species	AG	AI	AR	BE	BL	BS	FR	GE	GL	GR	JU	LU	NE	NW	OW	SG	SH	SO	SZ	TG	TI	UR	VD	VS	ZG	ZH	Number of Cantons (after 2000)
<i>Chelostoma distinctum</i>	•			•	•	•	•	•		•	•	•	•		•	•	•	•	•	•	•	•	•	•	•	•	20
<i>Chelostoma emarginatum</i>								○													•		○				3
<i>Chelostoma florisomme</i>	•	○	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	25
<i>Chelostoma foveolatum</i>										•											○		•	•	•		4
<i>Chelostoma grande</i>				•						○					○	○						•	•	•			7
<i>Chelostoma rapunculi</i>	•		•	•	•	•	•	•	•	•	•	•	•	•	○		•	•	•	•	•	•	•	•	•	•	25
<i>Coelioxys afer</i>	•			•	•	•	•	•			•		•	•			•	•			•		•	•	•	•	15
<i>Coelioxys alatus</i>										○							•	•		○		•		•			5
<i>Coelioxys aurolimbatus</i>	•			•		○	•	•		•	•	•	•	•		•	•	•	•	•	•		•	•	•	•	19
<i>Coelioxys conicus</i>	•			•	•		•	•	•	•		•	•	○		•	•	•		•	•	•	•	•	•	•	18
<i>Coelioxys conoideus</i>				•		○	○	•		○	•		•				○			○			•	•		○	13
<i>Coelioxys echinatus</i>	•			•	•			•		•			•				•	•			•			•			6
<i>Coelioxys elongatus</i>	•			•		•	•	•	•	•	•		•	•		•	•	•	•	•	•	•	•	•		•	19
<i>Coelioxys emarginatus</i>								○													•						1
<i>Coelioxys inermis</i>	•			•	•	•	•	•	•	•				○		•	•	•			•		•	•	•	•	16
<i>Coelioxys lanceolatus</i>				•					•	•				○		•						•		○	•		8
<i>Coelioxys mandibularis</i>	•	•		•			•		○	•				○		•	•				•		○	•	•	•	10
<i>Coelioxys rufescens</i>	•			•	•		•	○	•	•	•	•	•	•		•	•	•	•	•	•	•	•	•	•	•	22
<i>Colletes collaris</i>						○																					1
<i>Colletes cunicularius</i>	•			•	•	•	•	•		•	•	•	•	•		•	•	•	•	•	•	•	•	•	•	•	22
<i>Colletes daviesanus</i>	•			•	•	•	•	•		•	•	•	•			•	•	•	•	•	•		•	•	•	•	18
<i>Colletes floralis</i>										•											•						3
<i>Colletes fodiens</i>						○		○		○											•				•		5
<i>Colletes gallicus</i>								○													•		○				2
<i>Colletes hederæ</i>	•			•	•	•	•	•		•	•	•	•								•		•	•	•	•	22
<i>Colletes impunctatus</i>				•					•	•											•						6
<i>Colletes marginatus</i>								○	•	•											•						4
<i>Colletes mlokosewiczii</i>								○		○																	2
<i>Colletes nigricans</i>								○																			2
<i>Colletes sierrensis</i>																					○						2
<i>Colletes similis</i>	•			•	•	•	•	•		•	•	•	•								•		•	•	•	•	21
<i>Colletes succinctus</i>								○		•											•						4
<i>Dasypoda argentata</i>										○																	2
<i>Dasypoda hirtipes</i>				•			•	•		•							•	•	•		○		○	•	•	○	11
<i>Dioxys cinctus</i>				•				○		•			○								•		○	•	•	○	9
<i>Dufourea alpina</i>				•					•	•				•							•		•	•	•		9
<i>Dufourea dentiventris</i>				•				○		•				•			○	○	○	○	•		•	•	•	•	13
<i>Dufourea halictula</i>																											1
<i>Dufourea inermis</i>				○						•											○		•		•		5
<i>Dufourea minuta</i>				○						•			○				•							•	•		5
<i>Dufourea paradoxa</i>				•						•						○					•		•	•	•		6
<i>Epeoloides coecutiens</i>	•						•	•		•	•	•					○	○	○		•		•	•	•	•	17
<i>Epeolus alpinus</i>				•				○		•					○								○		•		6



Species	AG	AI	AR	BE	BL	BS	FR	GE	GL	GR	JU	LU	NE	NW	OW	SG	SH	SO	SZ	TG	TI	UR	VD	VS	ZG	ZH	Number of Cantons	Number of Cantons (after 2000)
<i>Epeolus cruciger</i>	•			•		○	•	•	•	•							•	•	•	•	•	•	•	•	•	•	13	12
<i>Epeolus fallax</i>				•																							1	1
<i>Epeolus productulus</i>																								•			1	1
<i>Epeolus variegatus</i>	•			•	•	•	•	•	•	•	•	•	•			•	•	•	•		•	•	•	•	•	•	18	18
<i>Eucera hungarica</i>																								○			1	0
<i>Eucera interrupta</i>								○								•					•			•			4	3
<i>Eucera longicornis</i>	•			•	•	○	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	23	22
<i>Eucera nigrescens</i>	•	•	○	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	25	24
<i>Eucera nigrifacies</i>								•													•						2	2
<i>Eucera pollinosa</i>										•											•			○			3	2
<i>Halictus carinthiacus</i>				•			•						•										•				5	5
<i>Halictus confusus</i>	•			•	•	○	•	•	•	•		•	•	•		•	•	•	•		•	•	•	•		•	17	16
<i>Halictus eurygnathus</i>	•			•	•			•	•	•	•		•				•	•			•	•	•	•	○		12	11
<i>Halictus fulvipes</i>											•										○						1	0
<i>Halictus kessleri</i>								○																○			2	0
<i>Halictus langobardicus</i>	•			•	•	•	•	•		•	•	•	•	•				○	•		•		•	•		•	15	14
<i>Halictus leucaheneus</i>					•					•								○					•	•		○	5	4
<i>Halictus maculatus</i>	•			•	•	•	•	•		•	•	•	•			•	•	•	○		•	•	•	•	•	•	20	19
<i>Halictus quadricinctus</i>	•			•	•			•		•			•			•	•				•		○				10	9
<i>Halictus rubicundus</i>	•	•		•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	26	26
<i>Halictus scabiosae</i>	•	•		•	•	•	•	•	•	•	•	•	•	•		•	•	•	•	•	•	•	•	•	•	•	24	24
<i>Halictus seladonius</i>								○													•						3	2
<i>Halictus sexcinctus</i>	○			•			•	○		•		○	•	•			•	•	○		•		•	•		•	14	10
<i>Halictus simplex</i>	•			•	•	○	•	•		•	•	•	•	•			•	•	•	•	•	•	•	•	•	•	22	21
<i>Halictus subauratus</i>	•			•	•	•	•	•		•	•	•	•	•			•	•	•	•	•	•	•	•	•	•	21	21
<i>Halictus submediterraneus</i>					•	•				○																•	5	4
<i>Halictus tectus</i>																								○			1	0
<i>Halictus tumulorum</i>	•	•		•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	26	26
<i>Heriades crenulata</i>	•			○	•			•		○		•									•		○			•	10	7
<i>Heriades rubicola</i>						•															•						3	2
<i>Heriades truncorum</i>	•		•	•	•	•	•	•	•	•	•	•	•	•	○		•	•	•	•	•	•	•	•	•	•	25	24
<i>Hoplitis acuticornis</i>								○													•		•	•			2	1
<i>Hoplitis adunca</i>				•	•	•	•	•	•	•	•	•	•	•	○		•	•	•		•	•	•	•	•	•	23	22
<i>Hoplitis anthocopoides</i>				○			○	○		○			○				○	○	•			•	•	•		○	9	2
<i>Hoplitis claviventris</i>	•	•	•	•	•		•	•	•	•	•	•	•	•	○		•	•	•	•	•	•	•	•	•	•	25	24
<i>Hoplitis dalmatica</i>										•											•						3	3
<i>Hoplitis lepeletieri</i>				•			•	○		•					○						•	•	•	•			10	7
<i>Hoplitis leucomelana</i>	•			•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	24	24
<i>Hoplitis loti</i>		•		•			•		•	•		•	○	•					•		•	•	•	•			14	13
<i>Hoplitis mitis</i>		•		•			○	○		•		•	○	•		•			○		•	•	•	•		•	15	10
<i>Hoplitis papaveris</i>								○																			2	0
<i>Hoplitis praestans</i>							•							•													1	1
<i>Hoplitis ravouxi</i>	•			•	•		•	•		○	•	•	•	•				○	•				•	•		○	14	11



Species	AG	AI	AR	BE	BL	BS	FR	GE	GL	GR	JU	LU	NE	NW	OW	SG	SH	SO	SZ	TG	TI	UR	VD	VS	ZG	ZH	Number of Cantons (after 2000)
<i>Hoplitis robusta</i>										•						•							•				3
<i>Hoplitis stecki</i>									○																		1
<i>Hoplitis tridentata</i>	•			•	•	•	•	•		•	•	•					•		○		•		•	•	•	•	15
<i>Hoplitis tuberculata</i>			○	•			○		•	•		•			○			○			•		•	•	•		16
<i>Hoplitis villosa</i>		•		•			•			•		•				•		•	•	•	•	•	•	•	•		17
<i>Hylaeus alpinus</i>				•			•			•		•				•					•	•	•	•	○	○	10
<i>Hylaeus angustatus</i>				•			•	•		•			•			•	•	○			•	○	•	•	○	○	10
<i>Hylaeus annulatus</i>				•				•	•	•						•					•	•	•	•			8
<i>Hylaeus bifasciatus</i>								○																			9
<i>Hylaeus brevicornis</i>	•			•	•	•	•	•	•	•	•	•	•			•	•	•	•	•	○	•	•	•	•	•	0
<i>Hylaeus cardioscapus</i>										•						•	•	•	•	•	•	•	•	•	•	•	23
<i>Hylaeus clypearis</i>	•			•	•	○	•	•		•	•		•				•	•	•	•	•		•	•	•	•	1
<i>Hylaeus clypearis</i>				•	•		•	•		•	•		•				•	•	•	•	•		•	•	•	•	16
<i>Hylaeus communis</i>	•		•	•	•	•	•	•		•	•	•	•			•	•	•	•	•	•	•	•	•	•	•	25
<i>Hylaeus confusus</i>	•			•	•	•	•	•	•	•	•	•	•			•	•	•	•	•	•	•	•	•	•	•	23
<i>Hylaeus cornutus</i>	•			•	•	•	•	•		•			•				•	•	•		•	•	•	•	•	•	15
<i>Hylaeus crassanus</i>									○												○		•	•	•	•	3
<i>Hylaeus difformis</i>	•			•	•		•	○	•	•	•	•			•	•	•	•	•	•	•	•	•	•	•	•	21
<i>Hylaeus dilatatus</i>	•			•	•	•	•	•	•	•	•		•			•	•	•	•	•	•	•	•	•	•	•	19
<i>Hylaeus duckei</i>	•			○		○	•	•										○					○				4
<i>Hylaeus euryscapus</i>								○																			1
<i>Hylaeus gibbus</i>	•			•	•	•	•	•	•	•		•	•			○					•		•	•	•	•	15
<i>Hylaeus glacialis</i>										•											•						2
<i>Hylaeus gredleri</i>	•			•	•	•	•	•		•	•	•	•			•	•	•	•	•	•	•	•	•	•	•	22
<i>Hylaeus hyalinatus</i>	•			•	•	•	•	•	•	•	•	•	•		•		•	•	•	•	•	•	•	•	•	•	24
<i>Hylaeus incongruus</i>	•			•			•	•	•	•		•	○			•			•	•	•	•	•	•	•	•	15
<i>Hylaeus intermedius</i>								•		•											•						3
<i>Hylaeus kahri</i>	•			•	•	•	○	○	•	•			•			•	•				•	•	•	•	•	•	15
<i>Hylaeus leptocephalus</i>	•				•	•	○	•		○		•				•	•	○			○						11
<i>Hylaeus moricei</i>																○							•				2
<i>Hylaeus nigrinus</i>	•			•	•	•	•	•	○	•	•	•	•			•	•	•	•	•	•	•	•	•	•	•	22
<i>Hylaeus nivalis</i>				•					•	•		•				•		•			•	•		•			8
<i>Hylaeus paulus</i>	•			•			○			•		•				•	○		•				○				8
<i>Hylaeus pectoralis</i>				•			•									•	○										4
<i>Hylaeus pfankuchi</i>	•						•					•				•	•		•	•	•	•	•	•	•	•	12
<i>Hylaeus pictipes</i>	•				•			•		○		•	○										○				6
<i>Hylaeus pilosulus</i>							•					•															1
<i>Hylaeus punctatus</i>	•			•	•	•	•	•	•	•	•	•	•			•	•	•	•	•	•	•	•	•	•	•	23
<i>Hylaeus punctatissimus</i>	•			•		○	•	○		○		•	○			•	•				•		•	•	•	•	9
<i>Hylaeus rinki</i>	•			•					•	•		•				•	•	○	•		•	•	•	○			14
<i>Hylaeus signatus</i>	•			•	•	•	•	•	○	•	•	•	•			•	•	•	•	•	•	•	•	•	•	•	20
<i>Hylaeus sinuatus</i>	•			•	•	•	•	•	○	•	•	•	•			•	•	•	•	•	•	•	•	•	•	•	22
<i>Hylaeus styriacus</i>	•			•	•	•	•	•		•	•	•	○			•	•	•	•	•	•	•	•	•	•	•	20
<i>Hylaeus taeniolatus</i>	•			•	•			•		•		•				•	•	○			•		○				15



Species	AG	AI	AR	BE	BL	BS	FR	GE	GL	GR	JU	LU	NE	NW	OW	SG	SH	SO	SZ	TG	TI	UR	VD	VS	ZG	ZH	Number of Cantons	Number of Cantons (after 2000)
Hylaeus tyrolensis	•			•	•		•	•		•	•	•				•	•	•	•	•			○		•	○	13	11
Hylaeus variegatus	•			○		○		•		•	•		○								○		○		•	•	11	6
Icteranthidium laterale									○																•		3	1
Lasioglossum aeratum	•			•			○	○		•			○								•		•	•	•		9	6
Lasioglossum albipes	•	•	•	•	•	○	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	26	25
Lasioglossum albocinctum								•													○			•	•		3	2
Lasioglossum alpinum				•			•		•	•	•	•		•							○	•			•		11	9
Lasioglossum angusticeps	•							•																		2	2	
Lasioglossum bavaricum				•			•		•	•						•					○	•	•	•	•		9	8
Lasioglossum bluethgeni	•				•			•		•			•				•				•		•	•		•	8	8
Lasioglossum brevicorne								○		•											•	○			•		5	3
Lasioglossum breviventre				○															○					•	•		3	1
Lasioglossum buccale								○													•			•	•		3	2
Lasioglossum calceatum	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	26	26
Lasioglossum clypeare							○	•					○								○			•	•		5	2
Lasioglossum convexusculum				○		○		○		•			○								•				•		7	3
Lasioglossum costulatum	•			•	•	○	•	○		•	•	•					•		•	•	•				•	•	15	13
Lasioglossum cupromicans		•		•			•		•	•	•	•	•	•	•			•	•	•	•	•	•	•	•	16	16	
Lasioglossum discum										•											•			○		3	2	
Lasioglossum elegans								○																•	•	2	1	
Lasioglossum euboense								○															○		•	3	1	
Lasioglossum fratellum				•			•		•	•	•	•	•	•	•				•	•	•	•		•		15	15	
Lasioglossum fulvicorne	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	26	26
Lasioglossum glabriusculum	•			•	•	○	•	•		•	•	•	•				•	•	•	•	•		•	•	•	•	19	18
Lasioglossum griseolum								•															•	•	•	3	3	
Lasioglossum intermedium	•			•	○		•	•		•	•	•		•			•	•	•		•	•		•	•	•	18	17
Lasioglossum interruptum	•			•	•	•	•	•		•	○	•	•	•			•	•	•	○	•		•	•	•	•	19	17
Lasioglossum laeve				○		○		○					○											○	•		6	1
Lasioglossum laev dorsum							•			•											•				○		4	3
Lasioglossum laevigatum	•		•	•	•	○	•	•	•	•	•	•	○	•			○	•	•	•	•	•	•	•	•	•	25	21
Lasioglossum laterale																				○	•					1	1	
Lasioglossum laticeps	•			•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	24	24
Lasioglossum lativentre	•			•	•	•	•	•		•	•	•	•	•	•	•	•	•	•	•	•		•	•	•	•	21	21
Lasioglossum leucopus	•	•	•	•	•		•	○		•	•	•	•	•	•	•	○	•	•	•	•	•	•	•	•	•	24	21
Lasioglossum leucozonium	•		•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	25	25
Lasioglossum limbellum	•			•		•	•	•	•	•		•	•				○	•	•		○		•	•	•	•	18	16
Lasioglossum lineare	•			•	•	○	•	•		•	•	•	•	•	•	•	•	•	•				•	•	•	•	16	15
Lasioglossum lissonotum				○				○		•			○								○				•		6	2
Lasioglossum lucidulum	•			•			•	•		•	•	•	•	•			•	•	•	•	•		•	•	•	•	16	16
Lasioglossum majus	•			•			•	•		•											○			•	•	•	11	10
Lasioglossum malachurum	•			•	•	•	•	•		•	•	•	•		•		•	•	•	•	•	•	•	•	•	•	24	24
Lasioglossum marginatum	•			○	•	•		•			•	•	•				•	•	•		•		•	•	•	•	13	12
Lasioglossum marginellum								•					•				•	•	•		•		○		•	3	2	



Species	AG	AI	AR	BE	BL	BS	FR	GE	GL	GR	JU	LU	NE	NW	OW	SG	SH	SO	SZ	TG	TI	UR	VD	VS	ZG	ZH	Number of Cantons (after 2000)
Lasioglossum medinai				•								•	•				•	○		•	•		•				2
Lasioglossum minutissimum	•			•	•	•	•	•			•	•	•				•		○		•		•	•	•	•	15
Lasioglossum minutulum				•	•			○		•			•			○	•	•	•		•		•	•	•		11
Lasioglossum monstificum	•			•	•	•	•			•		•				•	○		•	•	•		•	•	•	•	15
Lasioglossum morio	•			•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	25
Lasioglossum nigripes	•		•	•	•	○	•	•	•	•	•	•	•			•	•	•	•	•	•		•	•	•	•	21
Lasioglossum nitidiusculum	•			•	○	○	•	•		•	•	•	•	•		•	•	•	•	•	•			•	•	•	20
Lasioglossum nitidulum	•			•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	○		•	•	•	•	•	•	24
Lasioglossum pallens	•			•	•	•	•	•	•	•			•			•	•	•	•	•	•		•	•	•	•	16
Lasioglossum parvulum	•			•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•		•	•	•	•		•	21
Lasioglossum pauperatum	○							○												○				○			4
Lasioglossum pauxillum	•			•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	24
Lasioglossum peregrinum													•								○						1
Lasioglossum pleurospectulum																○			•			•			•	•	4
Lasioglossum podolicum										•						•											3
Lasioglossum politum	•	•		•	•	•	•	•		•	•	•	•	•		•	•	•	•	•	•		•	•	•	•	20
Lasioglossum punctatissimum	•			•	•	•	•	•		•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	23
Lasioglossum puncticolle	•			•	•			•			•					•	•	•	•				•	○		•	11
Lasioglossum pygmaeum				○		○	•	•		•	•		•			•		•	•		•		•	•	•		12
Lasioglossum quadrinotatum								○		•											•			•	•	•	4
Lasioglossum quadrinotatum					○			○																○			0
Lasioglossum quadrisignatum						○		○									○					•					1
Lasioglossum rufitarse	•	•	•	•	•		•		•	•	•	•	•		•	•	○		•	•	•	•	•	•	○	•	23
Lasioglossum semilucens	•			•	•	•	•	•		•	•	•	•			•	•	•	•	•	•	•	•	•	•	•	20
Lasioglossum setulosum										•											•						2
Lasioglossum sexmaculatum										○																	1
Lasioglossum sexnotatum	○			•	•	○	○	○		•	•		○				○	•	•	○	•		○	•	•	○	16
Lasioglossum sexstrigatum	•			•			•	•		•		•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	17
Lasioglossum subfasciatum				○		○		○		○			○		○	○		○			○	○	○	•		○	2
Lasioglossum subfulvicorne				•						•			•		•	•					•			•	•		6
Lasioglossum subhirtum								•															•				2
Lasioglossum tarsatum							○			•											•			•			3
Lasioglossum transitorium										•											•						1
Lasioglossum tricinatum	•			•	•	•	•	•			•		•					•	•		•		•	•			12
Lasioglossum villosulum	•		•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•		•	•	•	•	25
Lasioglossum xanthopus	•			•	•	○	○	○		•			•			•	•	•	•	•	•			•	•	•	16
Lasioglossum zonulum	•			•	•	○	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	24
Lithurgus chrysurus								•		○											•						3
Macropis europaea	•			•	•	•	•	•		•	•	•	•			•	•	•	•	•	•	•	•	•	•	•	21
Macropis fulvipes	•			•	•		•	•		•	•	•		•		•	•	•	•	•	•	•	•	•	•	•	19
Megachile alpicola	•		•	•	•		○		•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	24
Megachile analis				•						•								○			•			•			6
Megachile apicalis					•	•		○		○											○			○			2



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Megachile argentata	•			•	•	•	•	•		○	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	20	19
Megachile centuncularis	•			•	•	•	•	•	•	•	•	•	•	•					•	•	•	•	•	•	•	•	23	23
Megachile circumcincta	•		•	•	•	•	•	•	•	•	•	•	•	•					•	•	•	•	•	•	•	•	23	23
Megachile ericetorum	•		○	•	•	○	•	•		•	•	•	•	•	•				•	•	•	•	•	•	•	•	25	23
Megachile flabellipes										○											•						2	1
Megachile genalis				○		○		○		•			○										•				1	1
Megachile lagopoda						○				•													•		○	○	9	4
Megachile lapponica										•						•							•		○	○	5	4
Megachile leachella								○		•											•						4	3
Megachile ligniseca	•			•	•	○	•	•	•	•	•	•						•	•	•	•	•	•	•	•	•	21	20
Megachile maritima	•			•		○	○	•		○	•		•					•		○	○	•	•	•	○		14	9
Megachile melanopyga							•			•									○		•						3	3
Megachile nigriventris	•		•	•	•	•	•	•	•	•	•	•	•	•	•			•	○	○	•	•	•	•	•	•	25	24
Megachile parietina	•		○	○	○	○	○	•		•			○					•	○	○	•		○			•	17	9
Megachile pilicrus										•						○					•				○		3	2
Megachile pyrenaea				•		○				•			•						○		•	•	•				10	7
Megachile pyrenaica				•		○	•	○		•		•	○		•						•	•	•	•			12	9
Megachile rotundata					•	•		•		•		•			•			•	•	•	•	•	•	•		•	12	12
Megachile sculpturalis	•							•		•		•									•	•				•	11	11
Megachile versicolor	•			•	•		•	•	•	•	•	•	•	•				•	•	•	•	○	•	•	•	•	22	20
Megachile willughbiella	•	•		•	•	•	•	•	•	•	•	•	•	•	•			•	•	•	•	•	•	•	•	•	26	26
Melecta albifrons	•			•	•	•	•	•		•	•	•	•	•				•	•		•	•	•	•	•	•	21	21
Melecta festiva										•		○	•								•						1	1
Melecta luctuosa				○		○	○	○		•			•								•		•				12	6
Melitta dimidiata									•	•																	2	2
Melitta haemorrhoidalis	•			•	•	○	•	•	•	•	•	•	•	•	•			•	•	•	•	•	•	•	•	•	23	22
Melitta leporina	•			•	•	•	•	•		•	•	•	•	•				•	•	•	•		•	•	•	•	18	18
Melitta nigricans	•			•	•	•	•	•		•	•	•	•	•				•	•	•	•	○	•	•	•	•	20	19
Melitta tricornis				•	•		○			•								•	•	•			•				8	7
Melitturga clavicornis																											1	1
Nomada alboguttata	•			•		○	•	○		•	•	•	•					•	•	•	•	•	•	•	•	•	19	17
Nomada argentata								○		•											•		○		○	•	6	3
Nomada armata	•			•	•	○	•	○		•		•	•						○		•	•	•	•		•	17	14
Nomada atroscutellaris	•			•	•		•	•		•		•	○					•	•	•	•		•	•		•	18	17
Nomada baccata								○		○									○					○			3	0
Nomada bifasciata	•			•	•	•	•	•		•	•	•	•					•	○	○		•	•	•	•	•	21	19
Nomada bispinosa																	○			○							2	0
Nomada blepharipes								○																			2	1
Nomada bluethgeni								○																			1	0
Nomada braunsiana						○		○		•											○			○		•	8	3
Nomada camifex				○				○																			1	0
Nomada castellana	•			○		•	○	○	•	•		○	○					•	•	○	○	•	•	•			16	10
Nomada confinis										•															○		1	0



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Nomada conjungens	●			●	●	○	○	●		●	○	○	●			●	●	●	●	●	○		●	●	●	○	18	12
Nomada connectens																								○		1	0	
Nomada discrepans								○																		1	0	
Nomada distinguenda	●			○	●	●	○	●		○									●		○		○	○	○	●	14	8
Nomada emarginata				○				○		●											○		●	●	●		8	5
Nomada errans				○		○	●	●		●								○		○			○			8	3	
Nomada fabriciana	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	25	25
Nomada facilis	●			●		○	●	○		●	●	●	●	●				●	●	○	●	●	●	●		19	16	
Nomada femoralis				○				○		●			○			●				○	●		○	○	○	○	10	4
Nomada ferruginata				●	●	○	●	●		●	●		○							○			●	●	●	○	12	8
Nomada flava	●		●	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	24	24
Nomada flavilabris																								○		1	0	
Nomada flavoguttata	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	26	26
Nomada flavopicta	●			●		○	●	●		●		●	●			●	●	●	●	●	●	●	●	●	●	●	18	17
Nomada fucata	●			●	●	○	●	●		●	●		●			●	●	●	●	●		●	●	●	●	●	18	17
Nomada fulvicornis	●			●	○	○	●	●		●	●	●	●	●		●	●	●	●	●	●		●	●	●	●	19	17
Nomada furva				○				○											●				○	●	○		3	1
Nomada fuscicornis										●								●						●		○	5	3
Nomada goodeniana	●			●	●	●	●	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	24	23
Nomada gransassoi				●						○														○	○		4	2
Nomada guttulata	○			●	●		○	○		●	●	●	●	●			●	●	●		●		●	●		●	16	13
Nomada hirtipes	●		●	●	●		○	●			●	●	●	●			●	●	●	●			●	●	●	●	17	16
Nomada integra	●		●	●	●	○	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	24	22
Nomada italica																								○		1	0	
Nomada kohli	●				●			●									●										4	4
Nomada lathburiana	●		○	●	●	●	●	●		●	●	●	●				●	●	●	●	○		●	●	●	●	20	18
Nomada leucophthalma				●		○	●	○		●		●	○	●			●	○	○	●	○	○	○	●	●	●	16	10
Nomada linsenmaieri														●									●	●	●		1	1
Nomada marshalli	●		●	●	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	○	●	25	23
Nomada mauritanica																					○			○		2	0	
Nomada melathoracica				○			○	○			○		○						○		○			○	○	○	10	1
Nomada minuscula								○													○					2	0	
Nomada moeschleri				●						●	●	●	●	●	●	●	●	●	●	●		●	●	●	●	●	13	13
Nomada mutabilis																										2	1	
Nomada mutica				○				○		●			○								●		●	●	●	●	7	4
Nomada nobilis																								●		1	1	
Nomada obscura				●										●				●						○		●	6	5
Nomada obtusifrons									●										○						●	4	3	
Nomada opaca				○		○														○					○	5	0	
Nomada panurgina								○																		2	0	
Nomada panzeri			●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	24	24
Nomada piccioliana				○						●							○		●		●				○	○	7	3
Nomada pleurosticta										●															●	2	2	



Species	AG	AI	AR	BE	BL	BS	FR	GE	GL	GR	JU	LU	NE	NW	OW	SG	SH	SO	SZ	TG	TI	UR	VD	VS	ZG	ZH	Number of Cantons	Number of Cantons (after 2000)
Nomada posthuma	●								●	●								●	●	○	●				●	7	6	
Nomada rhenana				○		○		●												○	○		○			6	1	
Nomada roberjeotiana						○		○																	○	3	0	
Nomada ruficornis	●		●	●	●	○	●	●	○	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	24	22	
Nomada rufipes				○				○	●	●				●							●					6	4	
Nomada sexfasciata	●			●	●	○	●	●		●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	20	19	
Nomada sheppardana	●			○	●		●	●		●	●	●				●	●	○	●	●	●		●	○	●	16	13	
Nomada signata	●			●	●	●	●	●		●	○	○	●			●	●	●	●	●	●	●	●	●	●	19	17	
Nomada similis				○					●	●											●	○			●	5	3	
Nomada stigma				○		○		○		●	●		○			○					○		○			10	2	
Nomada striata	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	24	24	
Nomada succincta	●			○		○	●	●		●		●	●	●		●	○			○	●		●	●		16	12	
Nomada tormentillae									●	●											○					4	2	
Nomada tridentirostris								○																		1	0	
Nomada villosa	●			○			○	○		●	●		○			●	○	○	○	●			●	●	○	15	8	
Nomada zonata	●				●			●	●	●	●	○	○								●		●	●	●	11	9	
Nomiapis diversipes								○													●	●				3	2	
Osmia alticola										●											●				●	3	3	
Osmia anceyi																							●			1	1	
Osmia andrenoides								○		●											○					10	6	
Osmia aurulenta	●	●	○	●	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	26	24	
Osmia bicolor	●	●		●	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●		●	●	●	●	24	23	
Osmia bicornis	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	26	26	
Osmia brevicornis	●			●	●	○	●	●		●	●	●				●	○	●	●	●	●	●	●	●	●	16	14	
Osmia caerulescens	●			●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	24	24	
Osmia cornuta	●			●	●	●	●	●		●	●	●	●				●	●	●	●	●	●	●	●	●	20	20	
Osmia gallarum	●			●	●		○	●		●	●		●				●	●	●	●	●		●	●	●	15	14	
Osmia inermis		●		●			●		●	●				●	●		○		●		●	●	○			13	10	
Osmia labialis		●		●			●	○		●	●	●		●	●			○			●	●	●		●	17	14	
Osmia latreillei								○																		2	1	
Osmia leaiana	●			●	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	23	23	
Osmia ligurica								○																		1	0	
Osmia mustelina		●		●			○	○	●	●			○	●	●			○	●	●	●	●	○			16	11	
Osmia nigriventris				●					●	●						●		○			●	○				8	6	
Osmia niveata	●			○	○	○	○	●	●	●	●	●	●	○			●	●	●	○	●	●	●	●	●	21	15	
Osmia parietina	●	●	●	●	●		●	○	●	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	23	22	
Osmia pilicornis	●			○			○	○				●	○				●	●	●	○			●			11	6	
Osmia rufhirta	●			●	●	○	●	●		●	●		●			○	●	●	●		●		●		●	16	14	
Osmia scutellaris										●											●					3	3	
Osmia spinulosa				●	○	●	●	●		●			●			●	●				●		●			13	12	
Osmia steinmanni				●			●		○	●			●		●											5	4	
Osmia submicans				●	●	○	○	●	●	●	●	○	●		●		○	●			●		●		○	18	12	
Osmia tergestensis																								●		2	1	



Species	AG	AI	AR	BE	BL	BS	FR	GE	GL	GR	JU	LU	NE	NW	OW	SG	SH	SO	SZ	TG	TI	UR	VD	VS	ZG	ZH	Number of Cantons (after 2000)
<i>Osmia uncinata</i>	●		●	●	●	●	●		●	●	○	●	●	○		●	●	●	○	●			○	●	●	●	19
<i>Osmia viridana</i>				●			○	○					●				○						●				6
<i>Osmia xanthomelana</i>	●	●	●	●	●	○	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	25
<i>Panurginus herzi</i>				●			○		●	●		●		●	●	●		●	●			●	○	●			12
<i>Panurginus montanus</i>								●	●	●																	2
<i>Panurginus sericatus</i>				●						●											●	●	●	●	●		5
<i>Panurgus banksianus</i>			●	●	●	○	○	○	●	●	●	●				●					●	●	●	●	●		13
<i>Panurgus calcaratus</i>	○			●		○	○	●		●			○			●	○	○		○	●	●		●	●	●	15
<i>Panurgus dentipes</i>				○	○	○		●					●					●					●				8
<i>Pasites maculatus</i>																					●			●			2
<i>Protosmia minutula</i>																							●	●			1
<i>Pseudoanthidium nanum</i>					●	●		●		●							○				●		●		●		8
<i>Rhodanthidium caturigense</i>																							●	●	●		1
<i>Rhodanthidium septemdentatum</i>				○				○		●											●		●		●		4
<i>Rhophitoides canus</i>						○				●																	2
<i>Rophites algrus</i>				○				●		●											○		●				6
<i>Rophites quinquespinosus</i>				●	●	○		○		●	●							●		○			●	●		○	12
<i>Sphecodes albilabris</i>	●			●	●	●	●	●		●	●	●	●	●		●	●	●		●			●	●	●	●	19
<i>Sphecodes alternatus</i>								○		○											●						3
<i>Sphecodes crassanus</i>	●																							○			1
<i>Sphecodes crassus</i>			●	●	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	24
<i>Sphecodes cristatus</i>						●																		○			2
<i>Sphecodes croaticus</i>	●				●			●			●		○					●		●		●	●			●	11
<i>Sphecodes dusmeti</i>																							●				1
<i>Sphecodes ephippius</i>	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	25
<i>Sphecodes ferruginatus</i>	●			●	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	23
<i>Sphecodes geoffrellus</i>	●		●	●	●	○	●	○	●	●	●	●	○	●		●	●	●	●	●	●	●	●	●	●	●	23
<i>Sphecodes gibbus</i>	●		●	●	●	●	●	●	●	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	24
<i>Sphecodes hyalinatus</i>	●		●	●	●		●	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	24
<i>Sphecodes longulus</i>	●			●	●	●	●	●		●	○	●	●	●		●	●	●	●	●	●		●	●	●	●	19
<i>Sphecodes majalis</i>	●				●			●			●		●				●		●				●				10
<i>Sphecodes marginatus</i>				○				○																			0
<i>Sphecodes miniatus</i>	●			●	○	○	●	●		●		●	●	○		●	●	●	●		●	○	●	●	●	●	18
<i>Sphecodes monilicornis</i>	●			●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●	●		●	●	●	●	20
<i>Sphecodes niger</i>	●			●	●	○	●	●		●	●	●	●	●		●	●	●	●	●	●		●	●	●	●	21
<i>Sphecodes pellucidus</i>	○			●			●	●		●						●		○		●	●		●	●	●	○	12
<i>Sphecodes pseudofasciatus</i>	●						●	●		○	●		●			●		●			●		●			○	11
<i>Sphecodes puncticeps</i>	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	24
<i>Sphecodes reticulatus</i>	●			●	●	●	●	●		●	●	●	●	●		●	●	●	●	●	●		●	●	●	●	20
<i>Sphecodes rubicundus</i>				●			●	●		●			●			●		●			●					○	10
<i>Sphecodes ruficrus</i>	●			●	●	○	●	●			○	●	●	●		●	●	●	●	●	●		●	●	●	●	17
<i>Sphecodes rufiventris</i>	●			○			●	●		●	●		○			●	●	○		●	●		●	●	●	●	15
<i>Sphecodes scabricollis</i>	●			●	●		●	●		●	●	●	○		●	●		●	●	●	●	●	●	●	●	●	21



Species	AG	AI	AR	BE	BL	BS	FR	GE	GL	GR	JU	LU	NE	NW	OW	SG	SH	SO	SZ	TG	TI	UR	VD	VS	ZG	ZH	Number of Cantons	Number of Cantons (after 2000)
Sphecodes schenckii	●			●	●			●	●	●	●	●				●	●	●	●	●	●		○	○	○	●	15	13
Sphecodes spinulosus								○		●										●				●	●		4	3
Sphecodes zangherii																					●			●	●		2	2
Stelis annulata																								○		1	0	
Stelis breviscula	●			●		○	●	○	●	●	●	●	●	●		●	●	●	●	○	●	●	●	●	●	21	18	
Stelis franconica				●					●	●						●					○	●			●	6	5	
Stelis minima				○					●	●								○			○		●		●	7	4	
Stelis minuta	●			○	●			○	●	●						●	○	●	●		○	●		●	●	12	8	
Stelis nasuta	○							○		●										○			○		○	7	2	
Stelis odontopyga				●																				●	●	2	2	
Stelis ornatula	●			●			●	●	●	●	●	●	●	●			●	●	●	●	●	●	●	●	●	18	18	
Stelis phaeoptera				●		○	●	○		●	●	●				●	○	○	○	○	●	●	●	●	○	15	9	
Stelis punctulatisima	●			●	●	●	●	●		●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	22	22	
Stelis signata	●	●		●			○	●	●	●		●	●			○	●	●	●	●		○	●	●	●	18	15	
Stelis similima																					●					1	1	
Systropha curvicornis								○		○											○			●		4	1	
Systropha planidens					○	○																				2	0	
Tetralonia alticincta								●													○					2	1	
Tetralonia dentata										○											●	●		●	●	3	2	
Tetralonia fulvescens								●													○			●	●	3	2	
Tetralonia inulae																					●					1	1	
Tetralonia malvae								●		○											○		○			4	1	
Tetralonia pollinosa																								○		1	0	
Tetralonia salicariae	●			●				●		●						●					●			●	●	7	7	
Thyreus hirtus																					●			●		1	1	
Thyreus histronicus										○											●					2	1	
Thyreus orbatus	●			●			●			●								○					●		●	8	7	
Thyreus ramosus																							○	●		2	1	
Thyreus truncatus																								●		1	1	
Trachusa byssina	●	●	●	●	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	26	25	
Trachusa interrupta								○		○														●	●	3	1	
Tripeolus tristis																					●			○		2	1	
Xylocopa iris							●	●	●	●	●										●		○		●	7	6	
Xylocopa valga	●			●	●	●		●		●			●				●				●		●	●	●	13	13	
Xylocopa violacea	●			●	●	●	●	●	●	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	20	20	
Total number	295	76	94	410	259	271	331	436	171	464	243	266	324	202	127	320	290	306	198	272	445	239	416	532	185	334	632	575
Total number (after 1999)	283	72	80	341	247	158	276	281	161	413	232	254	265	188	109	289	255	262	185	232	387	219	348	475	182	295		



***Andrena alutacea* Stöckhert, 1942**

The distinctiveness of *A. alutacea* from *A. proxima* (Kirby, 1802) has been confirmed recently (Schmid-Egger 2005; Schmidt et al. 2015; McLaughlin et al. 2023). In Switzerland, *A. alutacea* occurs in the Plateau, in the Rhine Valley north of Chur, in the Engadin, in the Val Müstair, and south of the Alps in Ticino as well as in the Mesolcina and Poschiavo Valleys. In addition, there are ancient records from the Reculet, France (three females, Natural History Museum, Geneva) and one possible record from the Salève (three male specimens, leg. Frey-Gessner, tentatively identified as *A. alutacea*, Natural History Museum, Geneva; identification in males is particularly challenging in this group). In Switzerland, *A. alutacea* is nearly always found in sympatry with *A. proxima*, except in the Lower Engadin, where only *A. alutacea* has been recorded. See also comments under *A. ampla* Warncke, 1967. An identification key for the three species of the *A. proxima*-group can be found in Schmid-Egger (2005).

***Andrena amieti* Praz, Müller & Genoud, 2019**

This widely distributed, alpine species has been described recently (Praz et al. 2019); an identification key with all central European species of this species group is included in the cited article.

***Andrena ampla* Warncke, 1967**

The distinctiveness of *A. ampla* from *A. proxima* has been confirmed recently (Schmid-Egger 2005; McLaughlin et al. 2023). *Andrena ampla* has a mosaic-like distribution in the Swiss Alps (Valais, some valleys in Ticino, some valleys in Graubünden) and forms several narrow contact zones with *A. proxima*; both taxa have so far not been found in sympatry (McLaughlin et al. 2023). The contact zone between Martigny and St-Maurice (Valais) is only a few kilometers wide, and no hybrid specimen has been found (McLaughlin et al. 2023). Another contact zone is found in the Chur Region (Graubünden). *Andrena alutacea* and *A. ampla* have also never been found in sympatry. An identification key for the three species of the *A. proxima*-group present in Europe can be found in Schmid-Egger (2005).

***Andrena assimilis* Radoszkowski, 1876**

Following Wood and Monfared (2022), *A. gallica* Schmiedeknecht, 1883 is treated as a synonym of *A. assimilis*.

***Andrena barbareae* Panzer, 1805 and *A. cineraria* (Linnaeus, 1758)**

*Andrena barbareae* and *A. cineraria* have mostly been treated as distinct species (Gusenleitner and Schwarz 2002; Amiet et al. 2010), although Warncke (1986) treated *A. barbareae* and *A. cineraria* as synonyms. The

distinctiveness of these two species was recently shown using multi-locus genetic data (Gueuning et al. 2020), even if both taxa share DNA barcodes in central Europe (Schmidt et al. 2015; Gueuning et al. 2020). In Switzerland, a morphological separation of some Alpine populations is ambiguous. It is possible that some of these populations present some degree of introgression between both species. Also, whether both species are present in sympatry remains to be established. In particular, *A. cineraria*, although widely distributed at low elevation in northern Switzerland, has not been reported from mid-elevation sites in the Valais where *A. barbareae* occurs. This pattern suggests that these two taxa may be in an early phase of the speciation process, and that some reproductive interference may still prevent their presence in sympatry.

***Andrena bicolor* Fabricius, 1775**

The distinctiveness of *A. bicolor* from *A. allosa* and *A. amieti* is discussed under these two species (see above). According to previous genetic analyses (Schmidt et al. 2015; Praz et al. 2019; Gueuning et al. 2020), what has so far been considered as “*Andrena bicolor*” may represent two distinct cryptic taxa, both of which are widely distributed across Europe. These two taxa have distinct DNA barcodes and are mostly distinct based on nuclear genetic sequences (Gueuning et al. 2020). Based on available DNA barcodes, the most widely distributed form or taxon is distributed throughout Europe (Barcode Index Number, hereafter “BIN” **BOLD:AAD0134**) and is present in all biogeographic regions in Switzerland (Suppl. material 5, upper clade in *A. bicolor*). The second form (BIN **BOLD:AAD0135**; lower clade in Suppl. material 5) has been recorded, among other countries, in the UK, in Portugal, Spain, Germany, France and Greece; in Switzerland, it has so far only been reported from the Valais in spite of extensive barcoding in other regions, suggesting different climatic preferences in these two cryptic taxa. Since these nearly cryptic forms are currently not associated with names, and since there are still uncertainties on their taxonomic status, they are so far not treated as distinct species in the Swiss database. Numerous names have been proposed from the UK by Kirby (e.g., *Andrena gwynana* (Kirby, 1802)), where both cryptic taxa supposedly occur; future work is needed to further delineate species in this group, to determine the geographic distribution of each taxon, and to associate each taxon with a name, possibly through the designation of barcoded neotypes.

***Andrena bimaculata* (Kirby, 1802)**

Amiet et al. (2010) mention that this species occurs in three forms in Switzerland: form 1 with terga 2 and 3 (partly) red, legs dark; form 2 with terga dark and legs red; and form 3 with terga and legs dark. The names given to these forms by Amiet et al. (2010) are incorrect (Schmid-Egger 2012). Form 1 is restricted to the valleys



south of the Alps, where it occurs in sympatry with form 3, whereas intermediate specimens between both forms are unknown. DNA barcodes from forms 1 and 3 in sympatry from several sites in Ticino did not reveal divergences between both (Suppl. material 5), suggesting that they simply represent color forms within the same biological species, in agreement with the general gradient in color observed elsewhere (Falk and Lewington 2015). We have not been able to examine specimens of Amiet's form 2 and believe these specimens to be misidentified specimens of *A. tibialis* (Kirby, 1802).

***Andrena confinis* Stöckhert, 1930, *A. congruens* Schmiedeknecht, 1884 and *A. dallatorrei* Clément, 1922**

These three species have so far been treated as conspecific in Switzerland (Amiet et al. 2010). Schmid-Egger (2012) mentions that the presence of *A. confinis* in Switzerland requires confirmation. The analysis of DNA barcodes by Schmidt et al. (2015) suggests that both taxa are distinct, although their published sequences of *A. confinis* and of *A. congruens* originated from populations in widely different geographic regions, possibly confounding species boundaries with isolation by distance. No sequence is available for the unclear taxon known as *A. dallatorrei*, known only from the Alps in Switzerland and Austria (see below).

Based on morphological criteria, we consider *A. confinis* and *A. congruens* to represent distinct species; these differences were confirmed by DNA barcodes from Ticino and the Geneva region (*confinis*) and the Alps (*congruens*) (Fig. 3). The Swiss material of these two taxa was entirely revised by one of us (MH) and suggests the following pattern: *A. confinis* was historically widely distributed in northern Switzerland, with numerous records on the Plateau between Lake Geneva and Schaffhausen, as well as in the Rhine Valley around Chur and northwards. The last record of *A. confinis* in northern Switzerland is of 1945. There is no historical record south of the Alps. Recently, *A. confinis* was found twice in the Geneva region; these records are confirmed by DNA barcodes. It is not clear whether the species has maintained undetected populations in that region, or whether it has recolonized this area from France, as other taxa in the Geneva region (e.g., *Tetralonia malvae* (Rossi, 1790)). In addition, *A. confinis* was recently found twice south of the Alps (Ticino and Bregaglia Valley, Graubünden); the record from Ticino was confirmed using DNA barcodes. In Switzerland, *A. confinis* has only been found at low elevations (below 1000m).

*Andrena congruens* is widely distributed in the western Alps and is present locally in Graubünden; there are isolated records in Ticino, mostly at intermediate elevations. Currently, *A. confinis* and *A. congruens* do not appear to occur in sympatry, although both taxa occur in Ticino. Historically however, there are records of *A. congruens* along the Jura between the Neuchâtel region and Solothurn (last record in the Jura in 1978), in a region with records of *A. confinis*. These historical specimens would

represent the first sympatric occurrence of *A. confinis* and *A. congruens* in Europe.

The status of the third taxon remains unclear. *A. dallatorrei* is characterized by conspicuous differences in vestiture (mostly the nearly entirely dark vestiture on the female clypeus), but also consistent sculptural differences (in particular, the margin of tergum 2, which is nearly impunctate in *A. dallatorrei*, and strongly and distinctly punctate in *A. congruens*). *Andrena dallatorrei* is also appreciably larger (body length 12 mm, compared to 10–11 mm in *A. congruens* and *A. confinis*). These differences correspond to interspecific differences in *Andrena*. *Andrena dallatorrei* is known from very few localities and nearly entirely from old (<1950) specimens, but numerous specimens exhibiting constant morphology are available from some of these localities. All localities are in the dry valleys of the Alps (Rhône Valley near Sierre, as well as some alpine localities in the Valais; Val Müstair; Rhine Valley near Chur; Engadin). The last Swiss record of this taxon is from 2003 in the Valais. In the absence of genetic data, we do not treat *A. dallatorrei* as a valid species, and correspondingly do not include this taxon in the checklist. Future work is urgently needed to settle the status of this restricted and possibly endangered Alpine bee taxon.

***Andrena decipiens* Schenck, 1861 and *A. flavilabris* Schenck, 1874**

*Andrena flavilabris* has long been treated as the first generation of *A. decipiens*. It was recently elevated to species rank based on congruent mitochondrial genetic divergences, and phenological and biological differences (Mandery et al. 2008). Both species occurred historically in Switzerland and appear to have gone extinct approximately in the same period in the early 1900s.

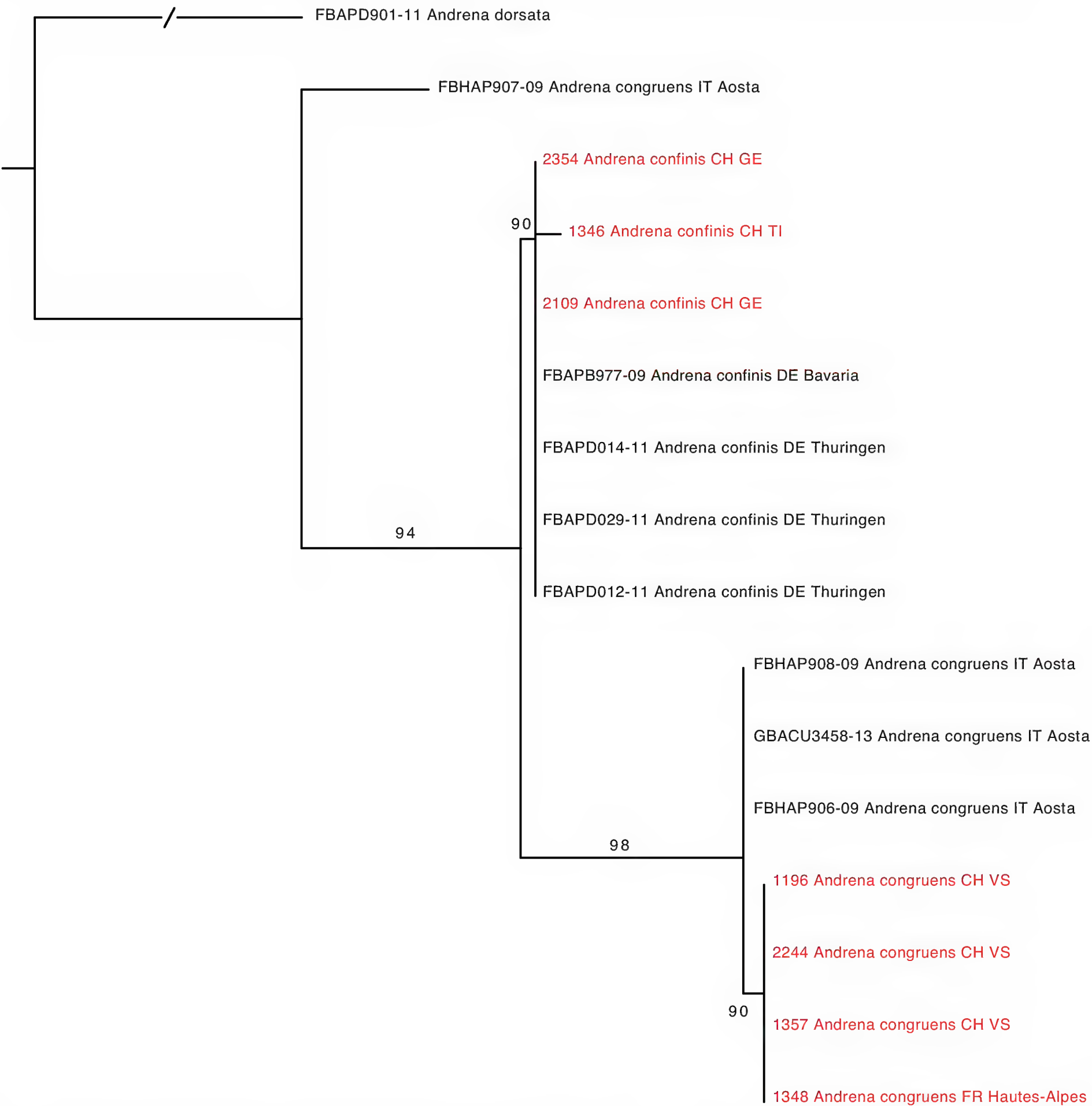
***Andrena dorsata* (Kirby, 1802) and *A. propinqua* Schenck, 1853**

The status of these two taxa has remained controversial (Gusenleitner and Schwarz 2002; Schmidt et al. 2015). A morphological separation of both taxa is mostly straightforward in Switzerland (Amiet et al. 2010), and the distinctiveness of these two taxa has recently been confirmed by an analysis of multi-locus genetic data (Gueuning et al. 2020). The lack of mitochondrial divergences highlighted by Schmidt et al. (2015) possibly relies on identification errors.

***Andrena floricola* Eversmann, 1852**

As indicated under *A. alfkenella*, the males of *A. floricola* and *A. alfkenella* have so far been misidentified in Switzerland. Most records of *A. floricola* from northern Switzerland indicated by Amiet et al. (2010) in fact belong to *A. alfkenella*. The distribution of *A. floricola* in Switzerland is currently restricted to the Valais, where the species is very rare. There are confirmed historical occurrences elsewhere in Switzerland (Geneva and Lausanne





**Figure 3.** Phylogenetic tree based on maximum likelihood analyses of the mitochondrial gene Cytochrome Oxidase I for individuals of *Andrena confinis* and *A. congruens*. Values above branches indicate bootstrap support values based on 1000 bootstrap replicates (values below 50 are omitted). The tree was rooted on the branch leading to *Andrena dorsata*; this branch was shortened for better graphic representation. The two-letter code after the species name indicates the country where the specimen was collected; for specimens collected in Switzerland, the canton is also given as a two-letter code (see caption to Table 2).

Region, Jura near Neuchâtel, Basel, Schaffhausen, Rhine Valley near Chur). For the separation of *A. alfkenella* and *A. floricola* see under *A. alfkenella* as well as Schmid-Egger and Scheuchl (1997) and Wood (2023a).

#### *Andrena florivaga* Eversmann, 1852

This species was first observed in Switzerland in 2015 (Bénon and Praz 2016), likely mirroring the range expansion of this species in Europe (e.g., Mandery 1999). *Andrena florivaga* is included in the key of Schmid-Egger and Scheuchl (1997); see also Bénon and Praz (2016).

#### *Andrena fulvicornis* Schenck, 1853

This taxon was treated as a synonym of *A. nitidiuscula* Schenck, 1853 by Amiet et al. (2010). It has recently been reported from northern Switzerland (Bénon and Praz 2016), where it has been observed a few times from 2015 onwards. We obtained DNA barcodes for three specimens identified as *A. fulvicornis* based on morphology; these three DNA barcodes were identical to available sequences of *A. fulvicornis*, and distinct from *A. nitidiuscula*, confirming the specific status of these two taxa (Suppl. material 5). De Beaumont (1960) mentions that



both *A. fulvicornis* and *A. nitidiuscula* occur in western Switzerland; we have revised the entire museum material identified as *A. nitidiuscula* (including the specimens in the de Beaumont collection) and did not find specimens of *A. fulvicornis* collected before 2015. It must be stressed however that the identification of old specimens with lightened (light brown/brown orange) integument color is challenging. The presence of *A. fulvicornis* in Switzerland is thus possibly the result of a recent range expansion. For the separation of *A. fulvicornis* and *A. nitidiuscula* see Schmid-Egger and Scheuchl (1997) and Schwenninger (2013). A third species of this groups occurs in central Europe, *A. curvana* Warncke, 1965. This species was found in a restricted region in Baden-Württemberg (Schwenninger 2013), but so far not in Switzerland.

#### ***Andrena gelriae* van der Vecht, 1927**

Revision of the material deposited in the Swiss museums revealed that many of the occurrences published by Amiet et al. (2010) were based on misidentified females (Praz et al. 2022). Confirmed occurrences of this species are restricted to pre-1970 records in the Swiss Plateau, and recent occurrences in the north of Switzerland, in the region of Geneva, in Vaud and in the Valais. The identification of females is difficult and requires comparative material (see identification key in Praz et al. 2022).

#### ***Andrena hesperia* Smith, 1853**

Amiet et al. (2010) report one record from the Valais. We have not been able to find a specimen associated with this record, which is considered doubtful and has been deleted from the database. In Switzerland, this species has only been found in a few northwestern localities after 1986. This population appears to be widely separated from the nearest populations in southern France.

#### ***Andrena limata* Smith, 1853 and *A. nitida* (Müller, 1776)**

The status of these two species remains controversial. The mostly central to northern European species *A. nitida* is univoltine, while the mostly southern European species *A. limata* is bivoltine (Schmid-Egger and Scheuchl 1997; Amiet et al. 2010). In Switzerland, we are confident that two distinct species occur, the univoltine *A. nitida*, which is widely distributed, and a bivoltine taxon that has so far been referred to as *A. limata*. This bivoltine taxon is morphologically slightly distinct from *A. nitida* (Amiet et al. 2010), in both sexes and in both generations, although the differences are more pronounced in the second generation (there are only few confidently identified specimens of the first generation in collections). Morphological differences are mostly restricted to vestiture length (unclear in first generation) and colour: female: vestiture on face and mesonotum (especially posteriorly) shorter in *A. limata*; vestiture on sides of mesosoma yellowish-brown in *A. limata*, greyish-white in *A. nitida*; male: hairs on face and on sterna predominantly greyish-white in *A. nitida*,

dark in *A. limata*. Long series of this bivoltine taxon are available in historical collections from the Geneva area, from the southern Alps (Ticino, Mesolcina), as well as isolated records in the Swiss Plateau. Isolated specimens have been collected recently in the southern Alps (Ticino, Graubünden) and in the Engadin (Graubünden).

Two taxonomic issues persist in this group. First, the Swiss specimens attributed to *A. limata* are morphologically divergent from southern European specimens of *A. limata*; in the latter, the hairs on the thorax are even shorter, and there are additional subtle differences in the sculpture between Swiss and southern European *limata*. In some respects, the Swiss *limata* are intermediate between typical *nitida* and southern European *limata*, possibly leading Warncke (1986) to treat *limata* and *nitida* as two subspecies. Second, DNA barcodes also present ambiguous results with respect to the status of Swiss specimens of *limata*: we present DNA barcodes for three specimens of *A. limata*, one from southern Ticino, one from the Bregaglia Valley (Graubünden) and one from the Engadin, as well as one barcode of *A. nitida* from southern Ticino (Fig. 4), within the known range of *A. limata*. In agreement with morphology, DNA barcoding suggests minimal, but constant differences between *nitida* and *limata* in Switzerland, and divergences between the Swiss *limata* and the southern European *limata* (Fig. 4). We therefore recognize *A. limata* and *A. nitida* as distinct taxa but highlight that more research is needed to further delineate species at the European level in this group (see also Wood 2023a). In addition, we stress that the identification of some Alpine specimens is unclear; barcodes could not be obtained from these unclear specimens.

#### ***Andrena montana* Warncke, 1973**

The status of this species was confirmed by Praz et al. (2019), who provide data on its biology and distribution, and include *A. montana* in an identification key.

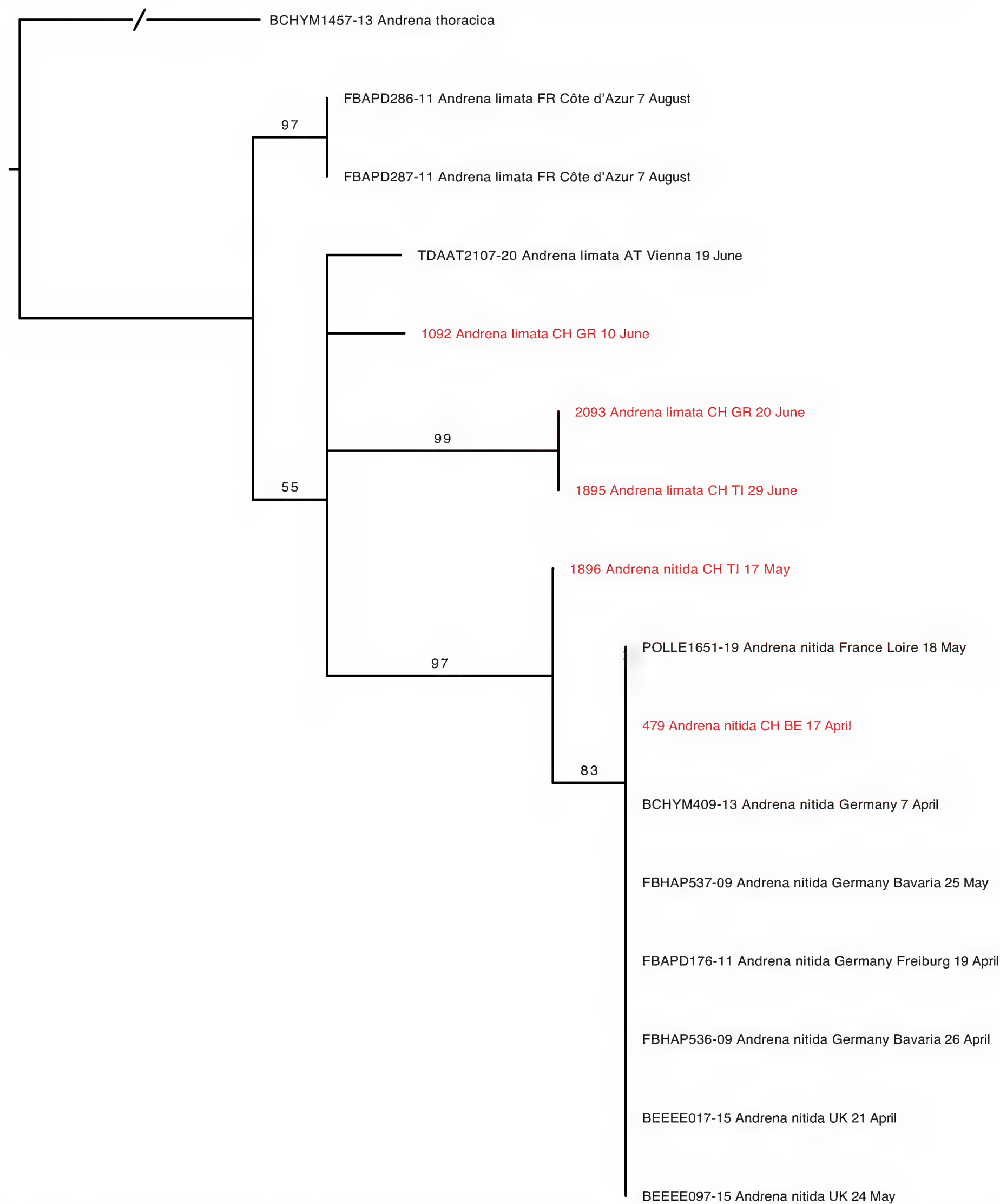
#### ***Andrena mucida* Kriechbaumer, 1873**

This Mediterranean species was so far only known from three specimens collected by H. Tournier and F. Chevrier, both in the Geneva region, rendering the isolated occurrence of this species near Geneva somehow doubtful, as this species is known in France only from the southern part of the country (Warncke et al. 1974). Six specimens collected on several occasions by Frey-Gessner in the Salève Region in France, just 10–20 km south of Geneva confirm the presence of this species in the Geneva region. Moreover, the species was collected by F. Amiet in St-Pierre, near Aosta in northern Italy, indicating that the Swiss records are not unique in central Europe.

#### ***Andrena nanula* Nylander, 1848**

Two records from the Bernese Alps and Geneva regions (Amiet et al. 2010) were based on a misidentified specimen and on a misinterpreted locality. This species is present in Switzerland only south of the Alps and in Graubünden.





**Figure 4.** Phylogenetic tree based on maximum likelihood analyses of the mitochondrial gene Cytochrome Oxidase I for individuals of *Andrena limata* and *A. nitida*. Values above branches indicate bootstrap support values based on 1000 bootstrap replicates (values below 50 are omitted). The tree was rooted on the branch leading to *A. thoracica*; this branch was shortened for better graphic representation. The two-letter code after the species name indicates the country where the specimen was collected; for specimens collected in Switzerland, the canton is also given as a two-letter code (see caption to Table 2); the collection day and month are also indicated.

***Andrena nigroolivacea* (Kirby, 1802)**

This species, first observed in Switzerland in 1991, has progressively expanded its distribution in northern Switzerland, where it now occurs between Yverdon and Lake Constance.

***Andrena nigrospina* Thomson, 1872 and *A. pilipes* Fabricius, 1781**

The status of both taxa has long remained controversial (Schmid-Egger and Patiny 1997; Gusenleitner and Schwarz 2002). Recent studies suggest that both taxa



differ in their genital morphology, vestiture colour, phenology and DNA barcodes in northern Europe (Falk and Lewington 2015; Else and Edwards 2018; Wood 2023b). In Switzerland, the bivoltine taxon (*A. pilipes*) occurs in the Valais; based on the only two known occurrences in Ticino, both of which are from the month of July, the bivoltine taxon likely also occurred historically in Ticino. Four specimens from Vaud, Geneva, and the region of Basel however, are from May and June, thus unlikely to be the bivoltine taxon. Morphologically, these specimens perfectly agree with *A. nigrospina* (Falk and Lewington 2015), in particular the narrow valve and the length of the antennal segments in males, and the color of the vestiture in both sexes. Accordingly, these specimens are attributed to *A. nigrospina*, which is newly added to the Swiss fauna. The last record of *A. nigrospina* in Switzerland is from 1958. Both taxa can be identified using the keys of Falk and Lewington (2015), Else and Edwards (2018), and Wood (2023b).

#### ***Andrena nuptialis* Pérez, 1902**

Some doubts remain on the taxonomic status of both generations of this species (Westrich 2018). In Switzerland, this taxon is clearly bivoltine; DNA barcodes from the two generations suggest that both generations belong to the same biological species (Suppl. material 5).

#### ***Andrena ovata* Schenck, 1853**

This taxon was resurrected from synonymy by Praz et al. (2022), who mentioned a single Swiss specimen from Ticino. Since then, seven additional specimens have been found in collections, all collected in region of Geneva around 1900. This species is included in the identification key given in Praz et al. (2022).

#### ***Andrena pauxilla* Stöckhert, 1935 and *A. pusilla* Pérez, 1903**

The taxonomy of the species of the subgenus *Micrandrena* is challenging, especially in the *pusilla-spreta* group of species. Recently Wood (2023a) placed *A. curtula* Pérez, 1895 in synonymy with *A. spreta* Pérez, 1895, confirmed that *A. pusilla* and *A. spreta* represent distinct taxa, and resurrected *A. pauxilla* from synonymy with *A. curtula* (or *A. spreta*) (see also Scheuchl and Schwenninger 2015). In Switzerland, *A. pusilla* is known from historical records from Ticino and the Lake Geneva region, as well as from a single recent specimen collected in Geneva (verified using a DNA barcode; Suppl. material 5), possibly representing a recent range expansion from France after local extinction. *Andrena spreta* has not been reported in Switzerland so far (the closest occurrences are in southern France in the Ardèche Département; see Suppl. material 5).

Schmid-Egger and Scheuchl (1997) mention the presence of *A. pauxilla* in the Valais, but we were not able

to examine specimens from that canton. However we found two females of *A. pauxilla* from the Geneva region (one in the collection Tournier from Peney and one in the Frey-Gessner collection from Genthod). This species is newly added to the Swiss fauna and represents another example of a species with isolated records in the Geneva region; there are confirmed records of this species in Germany, in southern France and in Spain (Wood 2023a). *Andrena pauxilla* is included in the identification key of Wood (2023a).

#### ***Andrena pellucens* Pérez, 1895**

This species was recently found in Ticino, probably following a range expansion from northern Italy (Bénon and Giollo 2022). One record from Geneva from the Tournier collection is considered dubious and is not accepted here, since the collection date (2.7.1876) is improbable for this autumnal species. Criteria for separating *A. pellucens* from *A. marginata* Fabricius, 1776 are indicated in Wood (2023a).

#### ***Andrena rosae* Panzer, 1801**

Based on the multi-locus genetic analyses of Gueuning et al. (2020), spring (*stragulata* Illiger, 1806) and summer (*rosae*) generations are treated as belonging to the same biological species.

#### ***Andrena rufula* Schmiedeknecht, 1883**

The two only records mentioned by Amiet et al. (2010) for Switzerland were based on misidentified specimens. This species was thus reported in Switzerland for the first time by Artmann-Graf (2017). Since then, this species has rapidly expanded its range and is now found between Vaud and the Zurich region. *Andrena rufula* is included in the identification key in Praz et al. (2019).

#### ***Andrena russula* Lepeletier, 1841**

Following Praz et al. (2022), *A. similis* Smith, 1847 is treated as a junior synonym of *A. russula*.

#### ***Andrena scotica* Perkins, 1916**

Following Wood et al. (2022), the univoltine taxon so far referred to as *A. carantonica* Pérez, 1902 is referred to as *A. scotica*; *Andrena carantonica* is treated as a nomen dubium. By contrast, Scheuchl et al. (2023) advocated for the continued use of *A. carantonica* for this taxon. In agreement with Wood et al. (2022), we consider that a morphological identification of the female lectotype of *A. carantonica* is not possible, and especially that both the original description (“fin juin et juillet sur les fusains (...) et surtout sur le tilleul argenté” [end of June and July on the European spindle, *Euonymus europaeus* L. and above all on the silver linden, *Tilia tomentosa* Moench])



and the manuscript catalogue to Pérez's collection (available at <https://science.mnhn.fr/catalogue/ey-bib-perez1/>) (“la femelle très commune dans la première quinzaine de juillet 1900, sur le *Tilia argentea*, (...) sur les fusains (...). Recueille le pollen de la ronce” [female very common during the first half of July 1900, on *Tilia argentea*, (...) on European spindels (...). Collect pollen from *Rubus*] refer with high likelihood to the summer brood of the taxon known as *Andrena trimmerana*.

#### ***Andrena taraxaci* Giraud, 1861**

With the possible exception of *A. stabiana* Morice, 1899 (see below), only one species of the *taraxaci*-group occurs in southern Switzerland. We do not know whether *A. pastellensis* Schwenninger, 2007 and *A. taraxaci* represent distinct species, and pending further investigation we continue to refer to this taxon as *A. taraxaci*. Following Schwenninger (2007), we consider the record from the Luzern region (see Amiet et al. 2010) as being based on mislabeled specimens.

#### ***Andrena tenuistriata* Pérez, 1895**

Two males were recently found in the Geneva region (one male has been barcoded; Suppl. material 5), probably following range expansion from France. This species is included in the key in Wood (2023a).

#### ***Andrena tscheki* Morawitz, 1872**

This species is known in Switzerland from a single male collected in Ticino by Frey-Gessner. Since Frey-Gessner's collection is reliable and given that the species is known from northern Italy (Gusentleitner and Schwarz 2002), this record is accepted.

#### ***Andrena trimmerana* (Kirby, 1802)**

Based on the multi-locus genetic analyses of Gueuning et al. (2020), spring (*spinigera* (Kirby, 1802)) and summer (*trimmerana*) generations are treated as belonging to the same species. This taxon is currently undergoing expansion in western and northern Switzerland, where it is now regularly found along the Jura and in the Plateau.

#### ***Anthidium florentinum* (Fabricius, 1775)**

This species was first reported in the Lugano region in Ticino in 2006 (Kouakou et al. 2008). Since then, the species has expanded its range in Ticino and the Mesolcina valley.

#### ***Anthidium loti* Perris, 1852**

This species was considered extinct by Amiet (1994). It was recently reported from southern Ticino, presumably following range expansion from northern Italy.

#### ***Anthophora canescens* Brullé, 1832**

This species is known from a single female collected in Genthod by Frey-Gessner. This record is specifically mentioned in Frey-Gessner's book. Since Frey-Gessner's collection is reliable, this record is accepted, even if this occurrence represents the only record of this species in central Europe.

#### ***Apis mellifera* Linnaeus, 1758**

Although this species is treated as an indigenous species, info fauna does not keep a database for *Apis mellifera* because: i. its presence is nowadays nearly entirely dependent upon apicultural activities and ii. hypothetical free-living populations are almost certainly strongly impacted by and intermixed with populations from apiaries (Parejo et al. 2020; Kohl et al. 2022).

#### ***Bombus distinguendus* Morawitz, 1869**

After several decades without observation in Switzerland, the species was recently found in the western Jura mountain range (Bénon et al. 2020). Given that it has been observed in the French Jura (e.g., Prost et al. 1987; Gilles Mahé, pers. comm., 2020), it is possible that this species was constantly present in the region, although at very low densities, but has remained undetected in the Swiss Jura between 1958 and 2019.

#### ***Bombus inexpectatus* (Tkalčů, 1963)**

This species, which was known in Switzerland from Ticino and Graubünden, was recently found in the Valais (Simplon region) in 2017.

#### ***Bombus jonellus* (Kirby, 1802)**

This species was recently found in three localities of the Swiss Jura; it is likely that the species has been overlooked in that region until now.

#### ***Bombus magnus* Vogt, 1911**

A single female of this species has been collected in Switzerland (Auvèrner NE, 1933, leg. de Beaumont; see Amiet et al. 2017). De Beaumont's collection is reliable, and the identity of the specimen has been verified using a DNA barcode (Suppl. material 5). Given that populations of this species have been recorded not far from Switzerland in France and Germany, we see no reason to question the validity of this record. It is probable that the vast, Ericaceae-rich peatbogs that once covered entire valleys in the Jura hosted populations of this species.

#### ***Bombus pascuorum* (Scopoli, 1763)**

South of the Alps, the female pilosity of *B. pascuorum* is bright red-orange on the mesosoma and metasoma, while



in other regions of Switzerland it is brown-orange intermixed with more or less black hairs on the mesosoma and on the terga. These geographic differences are rather striking, leading Amiet et al. (2017) to consider two subspecies to be present in Switzerland, *B. pascuorum pascuorum* south of the Alps and *B. pascuorum floralis* (Gmelin, 1790) in the rest of the country. For practical reasons, segregating two distinct subspecies is difficult, as transitional populations are known, e.g., in the Simplon region in the Valais. There is also substantial geographic variation north of the Alps; for example, some specimens of the Geneva region have no black hairs on the mesonotum, building a transition to the southern French populations. We see no advantage of recognizing subspecies for this species, and all specimens are lumped under a single taxon, *Bombus pascuorum*, in the Swiss database.

#### ***Bombus ruderatus* (Fabricius, 1775)**

This species has expanded its range in Switzerland after 2000. It is now widely distributed in the Swiss Plateau and was recorded for the first time in Graubünden in 2013. One worker (identification verified using DNA barcode; Suppl. material 5) was also collected in the Valais, suggesting that the species might currently be expanding its distribution in a region historically occupied only by *B. argillaceus* (Scopoli, 1763). Both taxa have however so far probably maintained non-overlapping distributions in Switzerland, since *B. argillaceus* has not been observed in the western parts of the Valais recently. The distance between the locality in the Valais where *B. ruderatus* has been observed, and the closest known population of *B. argillaceus* is only 20 km. Future research is needed to track the evolution of the distribution of both taxa in the Valais.

#### ***Ceratina nigrolabiata* Friese, 1896**

New record for Switzerland; two specimens were recently collected in Ticino, suggesting range expansion from Italy.

#### ***Chelostoma foveolatum* (Morawitz, 1868)**

Numerous recent records in the Valais (region of Martigny) and Vaud (region of Aigle) suggest a recent expansion or introduction. It is unlikely, though not impossible, that this species has so far remained undetected in this intensively sampled region.

#### ***Coelioxys conicus* (Linnaeus, 1758)**

This species is often referred to as *Coelioxys quadridentata* (Linnaeus, 1758) or *Coelioxys quadridentatus*. The case is similar to that of *Osmia bicornis* (Linnaeus, 1758) and *O. rufa* (Linnaeus, 1758), with both synonyms having been described in the same publication. For both cases, Kirby (1802), the first reviser, decided to use *Coelioxys conicus* and *Osmia bicornis*, respectively. By contrast, Dalla Torre (1896) selected the other name, presumably because of the so-called principle of page precedence, which is, however,

not a valid argument (see Day 1979). As in the case of *Osmia bicornis*, we propose to maintain *Coelioxys conicus* as the valid name for this taxon (see also Scheuchl et al. 2023).

#### ***Coelioxys emarginatus* Förster, 1853**

This species is known in Switzerland from a single female collected in Genthod by Frey-Gessner. Since Frey-Gessner's collection is reliable, this record is accepted here, even if it represents the only record in central Europe.

#### ***Epeolus alpinus* Friese, 1893**

One female of this species supposedly collected in Genthod (a locality near Geneva) by Frey-Gessner is preserved in the Geneva Natural History Museum. Unlike most other records from Frey-Gessner, the locality label is not original but has been recopied (Suppl. material 1: fig. S1C), and there is no date. Given that the known hosts of *E. alpinus* have never been recorded from Genthod or the Geneva region, we exclude this record. In Switzerland, this species is restricted to the Alps.

#### ***Epeolus fallax* Morawitz, 1872**

New record for Switzerland; this cuckoo bee associated with *Colletes hederæ* Schmidt & Westrich, 1993 was observed once in Switzerland in the canton Basel Landschaft (G. Artmann-Graf, pers. comm.).

#### ***Epeolus cruciger* (Panzer, 1799)**

Until 10 years ago, this species was very rare in Switzerland, where it was restricted to the southern parts of the country. Following the explosive spread of one of its hosts, *Colletes hederæ*, it currently shows a fast range expansion towards northern Switzerland.

#### ***Eucera interrupta* Baer, 1850**

New isolated records in Ticino and in the Rhine Valley in eastern Switzerland suggest a possible recent range expansion of this species, as has recently been observed in southwestern Germany (Burger and Reder 2018).

#### ***Eucera nigrifacies* Lepeletier, 1841**

New record for Switzerland; this species was first recorded in Ticino in 2017 and one specimen was found in the Geneva region in 2021. These two records suggest a recent northwards expansion of this southern European species.

#### ***Eucera pollinosa* Smith, 1854**

This species, previously considered to be extinct in Switzerland (Amiet 1994), was found in several localities in Ticino and in the Mesolcina valley (Graubünden) in 2020 and 2021, suggesting recent range expansion, as has recently been observed in Austria (Pachinger et al. 2019).



***Halictus confusus* Smith, 1853**

Two subspecies are recognized in central Europe: *Halictus confusus alpinus* Smith, 1853 and *H. confusus perkinsi* Blüthgen, 1926. In Switzerland, the former is present in most of the country (Alps, southern Switzerland and Swiss Plateau), while the latter is likely restricted to the north of the country, along the Rhine River between Basel and Schaffhausen (Amiet et al. 2001). The two taxa are difficult to separate, especially in the female sex (Ebmer 1969, 1988); moreover, they display transitional populations (Ebmer 1988), rendering their recognition as distinct taxonomic units complicated at the scale of a region that includes the contact zone. While we acknowledge that it may make sense to continue to recognize these two subspecies at the European scale, for example to highlight incipient speciation or the presence of possible cryptic species, their recognition in the Swiss database would be problematic given that most records are not identified to subspecific rank. The subspecies could simply be delimited based on geography, but we see no benefit of such an approach for conservation, at least as long as these two taxa are treated as conspecific.

***Halictus eurygnathus* Blüthgen, 1931**

This species is sometimes referred to as *Halictus compressus* (Walckenaer, 1802) (Pesenko 1985, 2004; Ghisbain et al. 2023). This case is complicated and, in our opinion, not yet resolved in a satisfactory manner. The name *Halictus compressus* was originally proposed as a *nomen novum* for the preoccupied taxon *Apis flavipes* Panzer, 1798. Another replacement name for the same taxon is *Hylaeus tomentosus* Herrich-Schäffer, 1840, which is the type species of *Monilapis* Cockerell, 1931. To settle the identity of *Monilapis*, Pesenko (1985) designated a neotype for *Apis flavipes* Panzer, 1798, selecting a male of the taxon known as *H. eurygnathus*. Most subsequent authors have not followed Pesenko's neotype designation (e.g., Ebmer 1988; Schwarz et al. 1996), arguing that *Apis flavipes* Panzer, 1798 is a *nomen dubium*, a view advocated recently by Scheuchl et al. (2023). While we agree that similarly resurrected names for unclear taxa should not be accepted (e.g., *Apis sabulosa* Scopoli, 1763 for *Andrena scotica*; see Wood et al. 2022; or *Apis ocreata* Christ, 1791 for *Andrena russula*; see Praz et al. 2022), the situation of *Halictus compressus* is different given the need to settle the identity of the type species of *Monilapis* for taxonomic stability, just as was done by Michener (1997) for the type species of *Tetralonia* (see comments below under *Tetralonia malvae*). In these two cases, the designation of a neotype and the resurrection of an old name may exceptionally be necessary for taxonomic stability. Awaiting further opinion on the matter, we continue to use the name *Halictus eurygnathus*.

Historically known only from the Alps, the region of Geneva and isolated records along the Jura and in the Swiss Plateau, *H. eurygnathus* has recently markedly expanded its range in northern Switzerland, where it is now regularly found along the Jura mountain range.

***Halictus fulvipes* (Klug, 1817)**

This southern European species has not been reported from Switzerland before (Amiet et al. 2001). A. Ebmer (pers. comm.) has examined a series of females collected in July 1954 in Brissago (Ticino), deposited in the Stockholm Natural History Museum. This occurrence is coherent with the distribution of this species in Europe (A. Ebmer, pers. comm.), and therefore this species is newly added to the Swiss fauna.

***Halictus seladonius* (Fabricius, 1794)**

This species so far known only in the Valais has recently been recorded from southern Ticino, probably following range expansion from northern Italy.

***Halictus submediterraneus* (Pauly, 2015)**

Pauly et al. (2015) investigated the *Halictus smaragdulus*-complex and concluded that several distinct species were present in Europe; only males can be identified with confidence using morphology. All the males that we examined from Switzerland belong to *H. submediterraneus*; as far as is known, other taxa of this group, such as *H. smaragdulus* Vachal, 1895, do not occur in Switzerland.

***Halictus tectus* Radoszkowski, 1875**

This species is sometimes treated as conspecific with *Halictus vestitus* Lepeletier, 1841 (Ghisbain et al. 2023; Reverté et al. in press; as *Seladonia vestita*). We follow Ebmer (1975, 1988) and treat *H. tectus* and *H. vestitus* as distinct taxa.

***Heriades rubicola* Pérez, 1890**

Historically only known from a single specimen from Sierre, this species was recently found in Ticino and in the Basel region, probably following range expansion, as reported elsewhere in Europe (Cross and Notton 2017; Saure and Wagner 2018). In both regions, the species was observed at several sites (Ticino) or during two different years (Basel), suggesting that populations are now established and reproducing.

***Hoplitis stecki* (Frey-Gessner, 1908)**

This species was resurrected from synonymy with *H. mucida* (Dours, 1873) by Müller et al. (2017).

***Hylaeus cardioscapus* Cockerell, 1924**

New record for Switzerland; this species was found in one site in Graubünden in 2020 and in 2021. Given that it is inconspicuous and belongs to a poorly sampled bee genus, it is difficult to know whether it has expanded its range recently, or whether it has always been present but remained undetected. *Hylaeus cardioscapus* is included in the identification key of Dathe et al. (2016).



***Hylaeus confusus* Nylander, 1852, *H. gibbus* Saunders, 1850 and *H. incongruus* Förster, 1871**

These three taxa have only recently been separated based on morphology (Straka and Bogusch 2011; Dathe et al. 2016). They have distinct DNA barcodes in central Europe (Schmidt et al. 2015). When the Swiss database was assembled for the genus *Hylaeus* (Amiet et al. 1999, 2014), *Hylaeus incongruus* was not recognized as a distinct species. One of us (RN) thus revised the entire available material of this group in Swiss collections and recognized three species, using the morphological criteria of Straka and Bogush (2011); morphologically unclear specimens were recorded as the *Hylaeus gibbus*-aggregate. We sequenced 58 specimens and obtained 55 usable DNA barcodes for these three species (Suppl. material 5). Of these 55 specimens, two were identified as the *Hylaeus gibbus*-aggregate based on morphology (meaning that the morphological criteria were unclear or inconsistent) and turned out to belong to *H. confusus* based on their DNA barcodes. The remaining 53 specimens were identified as *H. confusus* (38 specimens), *H. gibbus* (11) and *H. incongruus* (4) based on morphology. Assuming that the DNA barcodes provide correct identification, all specimens of *H. confusus* and *H. incongruus* were correctly identified; three specimens identified as *H. gibbus* turned out to belong to *H. incongruus*. We conclude that a morphological separation of these three species is mostly possible based on morphology, although a separation of *H. gibbus* and *H. incongruus* is sometimes difficult; based on our limited dataset, we estimate the identification error rate between these two species to be approximately 20% (3 specimens out of 15). Based on all specimens identified using morphology (which may thus include identification errors) the following patterns can be observed in Switzerland: *Hylaeus confusus* is by far the most common species (2556 occurrences), followed by *H. gibbus* (572 occurrences) and *H. incongruus* (239 occurrences). The three species are present in all biogeographic regions of Switzerland, although *H. gibbus* appears restricted to low-elevations, warm areas and is absent or rare at high elevations and along the northern flank of the Alps, unlike the other two species.

***Hylaeus euryscapus* Förster, 1871**

This species is known from five males collected in Peney between 1874 and 1885 (collection Tournier). Although this record is somehow isolated in central Europe, and although the species is not known in France near Geneva, the fact that the species was collected on five different occasions lead us to accept this record as valid. There are numerous other species with records near Geneva but no nearby record in France (see for example comments under *Andrena mucida*).

***Hylaeus glacialis* Morawitz, 1872**

Amiet et al. (2014) mention the presence of two morphological forms in Switzerland; these two forms could not be analyzed using DNA barcodes due to the rarity of this species in Switzerland. Future work is urgently needed to examine the taxonomic status of these two forms, which may represent cryptic, endangered species.

***Hylaeus intermedius* Förster, 1871**

Dathe et al. (2016) resurrected *H. intermedius* from synonymy with *H. gredleri* Förster, 1871. Based on their identification key and on pictures of the type specimens of *H. intermedius* and *H. imparilis*, the Swiss specimens hitherto referred to as *H. imparilis* Förster, 1871 (Amiet et al. 2014) appear to belong to *H. intermedius*. *Hylaeus imparilis* is probably a distinct species widely distributed in southern Europe but so far not found in Switzerland (R. Le Divelec, C. Praz, S. Schoder, in prep.). We have identified and sequenced specimens of *H. imparilis* from northern Italy (Aosta, St-Pierre) and from Ardèche, France (Suppl. material 5). *Hylaeus intermedius*, which was hitherto known only from south of the Alps in Switzerland, has recently been observed at several sites near Geneva, suggesting a recent range expansion.

***Hylaeus kahri* Förster, 1871**

This species forms two BINs in Switzerland. One BIN (**BOLD:AAN3379**) is distributed in the northern parts of the country (Basel), in the Valais, as well as in the Aosta Valley in northern Italy. Outside of Switzerland, sequences are available from Belgium, France, Germany and Spain. The second BIN (**BOLD:AAN3379**) is distributed only in Ticino and Graubünden (Mesolcina), south of the Alps. Outside of Switzerland, sequences are available from Italy and Austria, as well as some slightly divergent sequences from Greece. Based on sequences available on BOLD (Schmidt et al. 2015; Schoder 2018), the two BINs are found in near sympatry in the Aosta Valley and in Austria. The average genetic distance between these two BINs in Switzerland is 4.38% (range 3.51–5.40). Morphologically, specimens from these two BINs are identical and treated as conspecific for now (R. Le Divelec, C. Praz, S. Schoder, in prep.).

***Hylaeus moricei* Friese, 1898**

This species is sometimes referred to as *Hylaeus nigrifascies* (Bramson, 1879), a dubious name that was resurrected by Warncke (1972a, 1986). Dathe (1980) and Scheuchl et al. (2023) did not follow Warncke's view and maintained *Hylaeus moricei*. The matter is complicated by the fact that this taxon may actually be a complex of several closely related, cryptic species (Ghisbain et al. 2023), and if the taxon were to be split, the name that would eventu-



ally apply to central European populations is not yet clear (Ghisbain et al. 2023). For this reason, we prefer to continue to use the name *H. moricei* in the present checklist awaiting further taxonomic work on this group.

***Hylaeus pictipes* Nylander, 1852 and *H. taeniolatus* Förster, 1871**

The females of these two taxa are difficult to identify, although the criteria of Doczkal and Schmid-Egger (1992) mostly allow for an unambiguous identification if comparative material is used (Müller 2023). In the database, the females have been treated as a species aggregate until recently.

***Lasioglossum alpigenum* (Dalla Torre, 1877), *L. bavaricum* (Blüthgen, 1930) and *L. cupromicans* (Pérez, 1903)**

These three closely related species are treated as distinct following the clear morphological differences observed in the males (Ebmer 1988; Amiet et al. 2001), as well as the multi-locus genetic results of Gueuning et al. (2020). The females of *L. bavaricum* and *L. alpigenum* have not been separated in the database and are attributed to the *L. alpigenum/bavaricum*-aggregate. In some cases, the female of *L. cupromicans* are also difficult to separate from these two species. DNA barcodes can be used to discriminate *L. alpigenum* from the other two species (Suppl. material 5), which share DNA barcodes in Switzerland (Gueuning et al. 2020). Consequently, the combination of DNA barcodes and morphology mostly allows for a separation of the females of these three species.

***Lasioglossum angusticeps* (Perkins, 1895)**

This species was considered to be extinct in Switzerland (Amiet 1994; Amiet et al. 2001), but has since then been observed in the Geneva and Aarau regions, probably following range expansions from France and Germany, respectively. Based on limited available material to us (Suppl. material 5), the females are difficult to separate from those of *L. punctatissimum* (Schenck, 1853) with certainty; since only the latter species is widely distributed in Switzerland, a species aggregate has not been defined for these two species. Some records of *L. punctatissimum* in the area where *L. angusticeps* occurs may refer to that species.

***Lasioglossum fratellum* (Pérez, 1903) and *L. subfulvicorne* (Blüthgen, 1934)**

The females of these two species have not been separated in the Swiss dataset; they constitute the *L. fratellum-subfulvicorne*-aggregate. Males are however straightforward to tell apart. We barcoded 32 specimens of these two species (Suppl. material 5), of which two males of *L. subfulvicorne*. Although these two males appeared in one dis-

tinct clade, which could represent *L. subfulvicorne*, the rest of the specimens (presumably *L. fratellum*) formed a paraphyletic assemblage, and a clear separation of both taxa was not obvious. Future work is needed and additional males of these two species should be sequenced to examine whether DNA barcodes are diagnostic, as previously suggested based on a limited number of specimens (Schmidt et al. 2015).

***Lasioglossum medinai* (Vachal, 1895)**

This species has only recently been separated from *L. villosulum* (Kirby, 1802) (Pauly et al. 2019), although the presence of a cryptic taxon in this group has long been suggested (Packer et al. 1999). We have examined three females perfectly corresponding to the morphological criteria listed by Pauly et al. (2019) for *L. medinai*; two of these females were barcoded and were genetically similar to sequenced individuals of *L. medinai* (Pauly et al. 2019; Suppl. material 5). These limited results bring support for the validity of *L. medinai* and confirm its presence in Switzerland. The wide geographic distance between both occurrences of *L. medinai* in Switzerland and the occurrence of this species in ordinary habitats in the agricultural area, suggest that the species is probably more widely distributed than hitherto known in Switzerland.

***Lasioglossum monstificum* (Morawitz, 1891)**

Following Scheuchl and Willner (2016), we treat *Lasioglossum sabulosum* Warncke, 1986 as a junior synonym of *L. monstificum*.

***Lasioglossum tarsatum* (Schenck, 1868)**

This species was newly found in the Valais near Sierre; the identification of the specimens underlying this record has been verified using DNA barcodes (Suppl. material 5).

***Lithurgus chrysurus* Fonscolombe, 1834**

This species was recently observed in the Geneva region, probably following range expansion from nearby France. It was known before only from Ticino.

***Megachile argentata* (Fabricius, 1793)**

Following Praz and Bénon (2023), *Megachile pilidens* Alfken, 1924 is treated as a junior synonym of *Megachile argentata*.

***Megachile genalis* Morawitz, 1880**

Previously known from a single specimen from the Engadin, this species has recently been found in the Regional Nature Park Ela in Graubünden. The species is also known



in the French Jura, where it has been observed close to the border with Switzerland near Les Rousses (D. Genoud, pers. comm.) or near Pontarlier (C. Praz, pers. observation).

***Megachile sculpturalis* Smith, 1853**

This Asian species was first reported in Switzerland in 2010, and since then has colonized all biogeographic regions in Switzerland.

***Nomada alboguttata* Herrich-Schäffer, 1839**

*Nomada alboguttata* has long been suggested to represent a complex of several species (Amiet et al. 2007; Sann et al. 2010). A recent study based on multiple nuclear markers confirms that two distinct species co-occur in Switzerland, one associated with *Andrena ventralis* Imhoff, 1832 and mostly flying in April (form A) and one associated with *A. barbilabris* (Kirby, 1802) and flying in May and June (form B) (Mignot 2020). The Swiss material has not been revised and is thus so far treated as a single species in the database. Taxonomic research is also needed to determine to which taxon the available species names can be applied.

***Nomada bluethgeni* Stöckhert, 1943**

This species is known from a single female collected in Peney by Tournier. Since *Lasioglossum marginellum* Schenck, 1853, the only known host of this species has been collected repeatedly in the Geneva area, and based on the distribution of *N. bluethgeni* in Europe (southern France, Germany), the Swiss record is considered plausible and is accepted.

***Nomada confinis* Schmiedeknecht, 1882**

A single male of this species has been collected near Sierre in 1951 by M. Schwarz. There are no doubts on the origin of this specimen and this record is considered to be valid.

***Nomada discrepans* Schmiedeknecht, 1882**

Most records of this species indicated by Amiet et al. (2007) were based on misidentified specimens of *N. flavoguttata* (Kirby, 1802). Verified records of *N. discrepans* in Switzerland are restricted to a few correctly identified specimens from the Geneva region around 1900. *Nomada discrepans* is another example of a southern European species for which ancient records near Geneva represent the only central European records.

***Nomada fulvicornis* Fabricius, 1793 and *N. meridionalis* Schmiedeknecht, 1882**

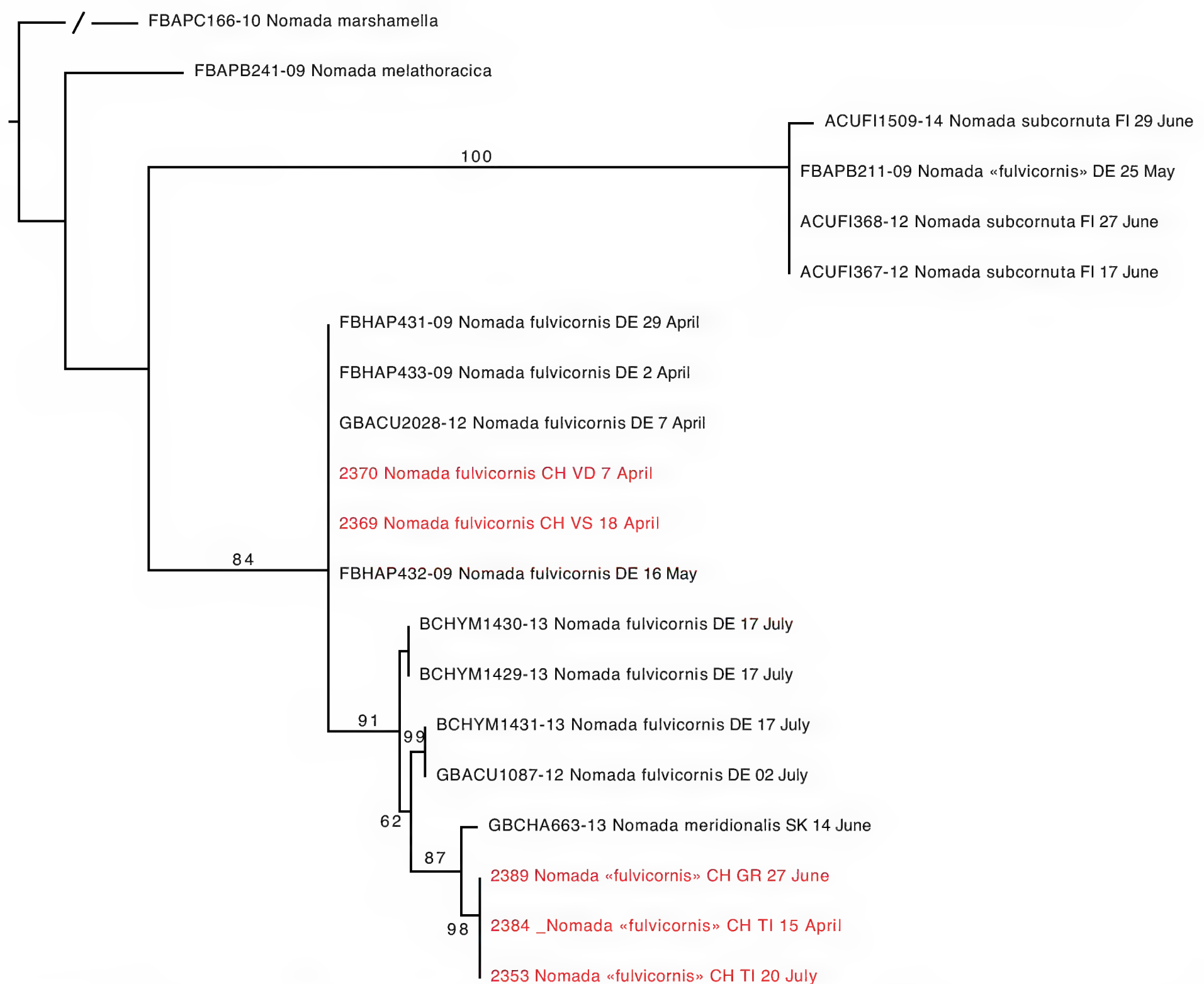
The status of these two forms remains controversial. Doczkal and Schmid-Egger (1992) mention that *N. meridionalis* occurs in sympatry with *N. fulvicornis* and list numerous morphological criteria to separate both taxa.

However, as indicated by Falk and Lewington (2015), the two generations of *N. fulvicornis* in England show conspicuous morphological differences, corresponding to the differences mentioned by Doczkal and Schmid-Egger (1992) to separate *N. meridionalis* and *N. fulvicornis*. Since all records of “*N. meridionalis*” in Doczkal and Schmid-Egger (1992) are from the summer, it is unclear whether the differences that they mention point to specific differences or to intergenerational variation. The host of the bivoltine *N. fulvicornis* in England is *A. bimaculata*, while the mostly univoltine form found in northern and central Europe is associated with the closely related, univoltine *A. tibialis*. Doczkal and Schmid-Egger (1992) mention that “*N. meridionalis*” is associated with *A. carbonaria* auct. (probably *A. pilipes* given the collection dates indicated) in Germany; Falk and Lewington (2015) report subtle morphological differences between populations of *N. fulvicornis* parasitizing *A. bimaculata* and those associated with *A. pilipes*. Based on DNA barcoding results, Schmidt et al. (2015) indicated that several BINs were present in Germany and in central Europe, one of them (represented by one specimen from Slovakia) corresponding to *N. meridionalis*.

In northern Switzerland, nearly all records of *N. fulvicornis* are from the spring and are most probably associated with *A. tibialis*, given that neither *A. pilipes* nor *A. bimaculata* is currently present in this region. In Ticino, there are spring and summer records of *N. fulvicornis*; the summer specimens are morphologically strongly divergent from the spring specimens, in agreement with the characters mentioned by Falk and Lewington (2015). DNA barcodes from specimens from northern Switzerland and from Ticino suggest some divergences; both spring and summer specimens from Ticino were identical to one another, and also very similar to the specimen of “*N. meridionalis*” sequenced by Schmidt et al. (2015). The phylogenetic tree (Fig. 5) suggests a clade of specimens from Finland and Germany collected in late spring/early summer (possibly *N. subcornuta* (Kirby, 1802); see below), then a clade (or cluster) of specimens collected in the spring from Germany and Switzerland, then a clade of specimens collected in the summer as well as one specimen from Ticino collected in April. This last clade possibly refers to “*Nomada meridionalis*”, even if it includes one specimen collected in the spring. Additional work is needed to determine: i. whether the differences in morphology mentioned by Doczkal and Schmid-Egger (1992) are due to intergenerational differences and ii. whether the univoltine (spring for one clade in *N. fulvicornis* and late spring/early summer for *N. subcornuta*) and bivoltine forms represent distinct species and whether they co-exist in sympatry; adding nuclear genetic data to the limited mitochondrial DNA barcode marker would be important.

One female from the Sierre region (Valais), collected in 20.07.1951 is morphologically identical to the summer form occurring in Ticino. This specimen was collected in a site where the bivoltine *A. pilipes* is present and was historically abundant (*A. bimaculata* is also present,





**Figure 5.** Phylogenetic tree based on maximum likelihood analyses of the mitochondrial gene Cytochrome Oxidase I for individuals of *Nomada fulvicornis* and closely related species. Values above branches indicate bootstrap support values based on 1000 bootstrap replicates (values below 50 are omitted). The tree was rooted on the branch leading to *Nomada marshamella*; this branch was shortened for better graphic representation. The two-letter code after the species name indicates the country where the specimen was collected; for specimens collected in Switzerland, the canton is also given as a two-letter code (see caption to Table 2); the collection day and month are also indicated.

although it is rare and has only been collected once in the Sierre region; *A. fuscata* Erichson, 1835 was also present in this site until 1973). A DNA analysis has not been performed on this old specimen. The sampling location is very close to one sequenced specimen of *N. fulvicornis* collected in the spring (number 2369 on Fig. 5). This finding possibly points to the sympatric occurrence (at least historically) of these two forms, one associated with *A. tibialis* and the other potentially with *A. pilipes*. Whether the form associated with *A. pilipes* is bivoltine, remains unknown. Given the uncertainties in the taxonomic status of “*N. meridionalis*”, this taxon is so far not recognized in Switzerland.

*Nomada subcornuta*, a form associated with the univoltine species *A. nigrospina* and *A. agilissima* (Scopoli, 1770), both of which are or were present in Switzerland, has recently been recognized as distinct (Falk and Lewington 2015). In Switzerland, there are some historical records (so far identified as “*N. fulvicornis*” in the database)

from the month of June in sites where *A. nigrospina* was present near Lausanne; these records may well belong to *N. subcornuta* and should be further investigated. Awaiting additional results, *N. subcornuta* is not currently considered to be present in Switzerland.

#### ***Nomada goodeniana* (Kirby, 1802) and *N. succincta* Panzer, 1798**

These two taxa mostly differ in their color pattern, which is variable geographically. In addition, DNA barcodes cannot always unambiguously separate these two species in Europe (Schmidt et al. 2015; Creedy et al. 2020). However, recent genetic and morphology analyses demonstrate that these two taxa are distinct in Germany and Switzerland (Diestelhorst and Lunau 2008; Gueuning et al. 2020), in agreement with previous analyses based on the chemical composition of mandibular gland volatiles and phenology (Kuhlmann 1997).



***Nomada kohli* Schmiedeknecht, 1882**

This species is in expansion in Switzerland; it has recently been observed in several localities in northern Switzerland and in the Geneva region.

***Nomada linsenmaieri* Schwarz, 1974**

We present two DNA barcodes of this species, one from a female specimen from the Valais, and one from a female specimen from Spain. The specimen from the Valais had an identical DNA barcode with *N. similis* Morawitz, 1872, but not the specimen from Spain (Fig. 6). Since the morphological identification of the Swiss specimen is not in doubt, this result suggests DNA barcode sharing (possibly following mitochondrial introgression) between *N. linsenmaieri* and *N. similis* in Switzerland, but not in Spain (Fig. 6).

***Nomada mauritanica* Lepeletier, 1841**

*Nomada chrysopyga* Morawitz, 1872 is treated as a junior synonym of *Nomada mauritanica* (Smit 2018).

***Nomada minuscula* Noskiewicz, 1930 and *N. sheppardana* (Kirby, 1802)**

The status of these two taxa remains controversial. Based on the morphological criteria of Amiet et al. (2007) and Smit (2018), we consider these two taxa to be distinct and present in Switzerland. DNA barcodes from Germany also suggested that these two taxa were distinct (Schmidt et al. 2015). In Switzerland, *N. minuscula* was until recently only known from historical records from the Geneva region and from one specimen from Ticino (1995). We examined one recently collected specimen from the Geneva region, morphologically perfectly corresponding to *N. minuscula*; the DNA barcode from that specimen, however, was identical to DNA barcodes of both *N. minuscula* and *N. sheppardana* (Fig. 7). This result suggests that unlike in Germany (Schmidt et al. 2015), these two taxa share DNA barcodes in southern Europe and in the Geneva region (Fig. 7). Further work is needed to examine whether the specimens identified as *N. sheppardana* from Germany belong to a distinct species from the Swiss and southern European specimens of *N. sheppardana*. For now, we treat *N. minuscula* and *N. sheppardana* as distinct species due to the rather clear morphological differences.

***Nomada mutabilis* Morawitz, 1871**

This species was recently newly recorded from the Müstair Valley (Graubünden).

***Nomada panzeri* Lepeletier, 1841**

Several distinct species are likely mixed in the *Nomada panzeri* species complex, including *Nomada glabella*

auct. nec Thomson, 1870 and another, unnamed species (Falk et al. 2022). Preliminary genetic work in Switzerland suggests the presence of four distinct species in this complex (Byrde 2022). Given the uncertainties surrounding the names applying to each of these species, and awaiting additional morphological and genetic evidence, only one species is recognized so far, *Nomada panzeri*, which includes the form so far referred to as *Nomada panzeri glabella* (Amiet et al. 2007; = *Nomada glabella* auct.; see Falk et al. 2022). An identification key to these forms is given in Falk et al. (2022).

***Nomada roberjeotiana* Panzer, 1799 and *Nomada tormentillae* Alfken, 1901**

These two closely related forms have often been referred to as a single species, *Nomada roberjeotiana*. In Switzerland, there are some scattered and ancient (all before 1900) records of *N. roberjeotiana* (sensu stricto) from the Swiss Plateau (regions of Geneva, Basel and Zurich), as well as some Alpine records of *Nomada tormentillae*. We generated DNA barcodes from one female of *N. tormentillae* from the Alps; this specimen originates from a site where numerous specimens of *Andrena tarsata* Nylander, 1848, the presumed host of *N. tormentillae*, were observed. This DNA barcode was highly similar to northern European DNA barcodes of *N. tormentillae* (average genetic distance 0.21%, range 0.16%–0.33%), and more divergent from sequences of northern European individuals of *N. roberjeotiana* (average distance 1.11%, range 1.09–1.20%). Although the divergence between *N. roberjeotiana* and *N. tormentillae* is weak and both species are included in the same BIN (Schmidt et al. 2015), this conserved differentiation at the continental scale strongly supports the recognition of these two taxa as different species. For the separation of *N. roberjeotiana* and *N. tormentillae* see Stöckert in Schmiedeknecht (1930) and Scheuchl (2000) (in the latter work, *N. tormentillae* is referred to as *N. montana* (Mocsáry, 1894)).

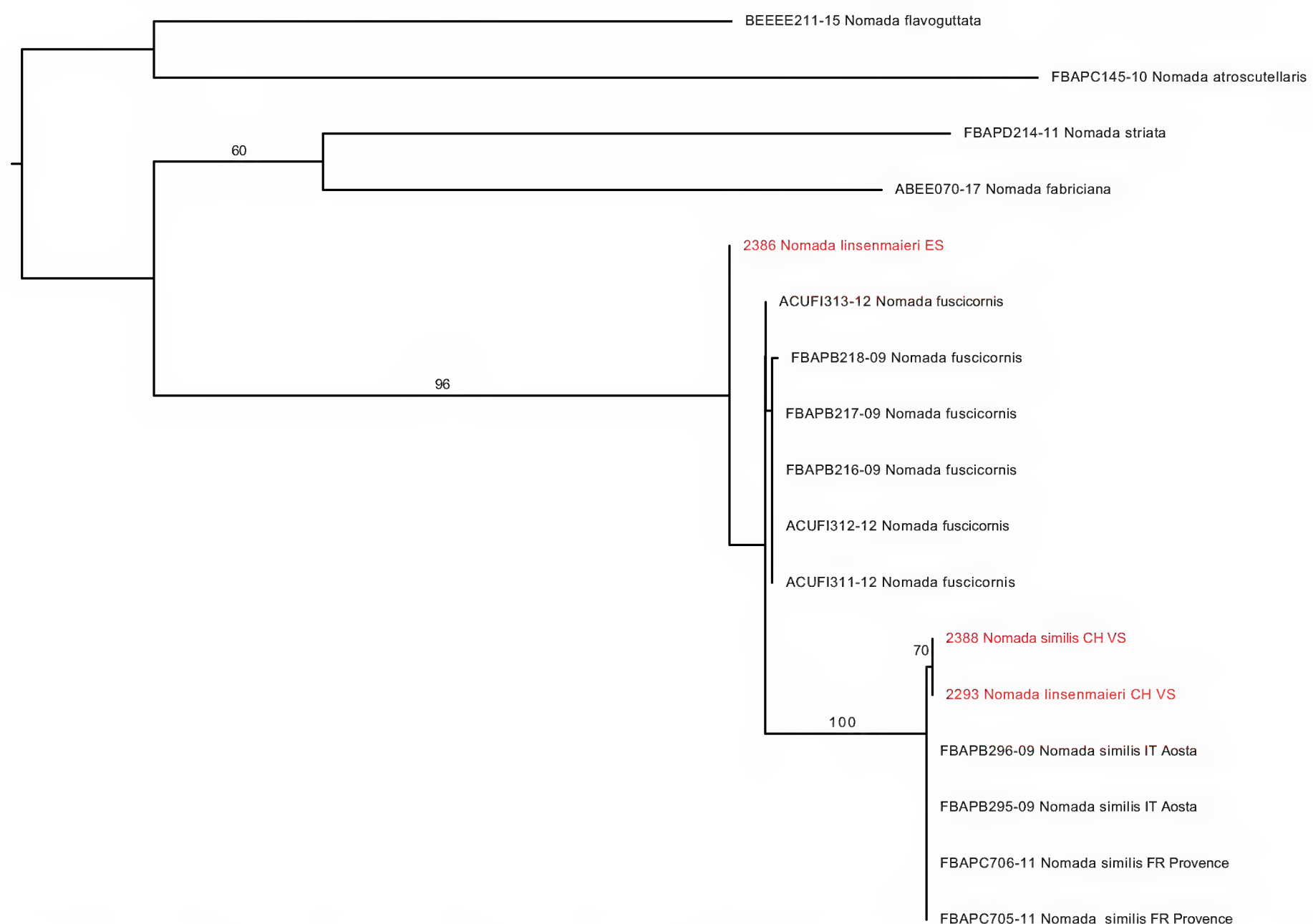
***Nomiapis diversipes* (Latreille, 1806)**

This species was recently recorded in Ticino, presumably following range expansion from northern Italy.

***Osmia latreillei* (Spinola, 1806)**

A few specimens of this species were collected by Tournier near Peney. This locality is the only central European locality for this southern European species. Given that Tournier collected several specimens on different dates, we believe that these records are correct; it is also unlikely that these records are based on temporarily introduced populations, for example due to the transport of nest-containing wood. In addition, one female was collected in Zurich in 2015; this record likely represents an accidental and temporary introduction of this species in central Europe (see also Reder (2000) for a similar, unique record in Germany).





**Figure 6.** Phylogenetic tree based on maximum likelihood analyses of the mitochondrial gene Cytochrome Oxidase I for individuals of *Nomada similis*, *N. linsenmaieri* and closely related species. Values above branches indicate bootstrap support values based on 1000 bootstrap replicates (values below 50 are omitted). The tree was rooted on the branch leading to *Nomada flavoguttata* and *N. atroscutellaris*. The two-letter code after the species name indicates the country where the specimen was collected; for specimens collected in Switzerland, the canton is also given as a two-letter code (see caption to Table 2).

### *Osmia ligurica* Morawitz, 1868

*Osmia ligurica* represents another species only collected by Tournier near Geneva. *Osmia ligurica* is present in central Europe near Aosta in northern Italy, rendering the Geneva record plausible.

### *Panurginus montanus* Giraud, 1861 and *Panurginus sericatus* (Warncke, 1972)

The two Alpine taxa *Panurginus (montanus) sericatus* and *P. (montanus) montanus* have alternatively been recognized as subspecies or as distinct species (Warncke 1972b, Schwarz and Gusenleitner 1997; Ebmer 2001; Amiet et al. 2010). These two taxa differ in the shape of the gonostylus. In Switzerland, *P. (montanus) sericatus* is distributed in the entire Alpine bow except for its easternmost part and hardly overlaps in its distribution with *P. montanus s. str.*, which occurs in the easternmost part of Graubünden, mostly east from the Rhine River and from Chur. According to Amiet et al. (2010), the populations in the Bernina region are intermediate between both taxa, suggesting a recognition only as two subspecies of a broad *P. montanus*. However, a population of *P. montanus s. str.* was recently uncovered near Glarus, expanding the known distribution of this taxon in Switzerland. This finding leads us to treat both taxa

as separate species. We interpret the deviating morphology of the populations in the Bernina region as morphological variability within *P. sericatus*, rather than a sign of transitional morphology between two subspecies. Future work is needed to examine species boundaries in this complex.

### *Pasites maculatus* Jurine, 1807

This species was recently recorded in Ticino, presumably following range expansion from northern Italy along with its host *Nomiapis diversipes*.

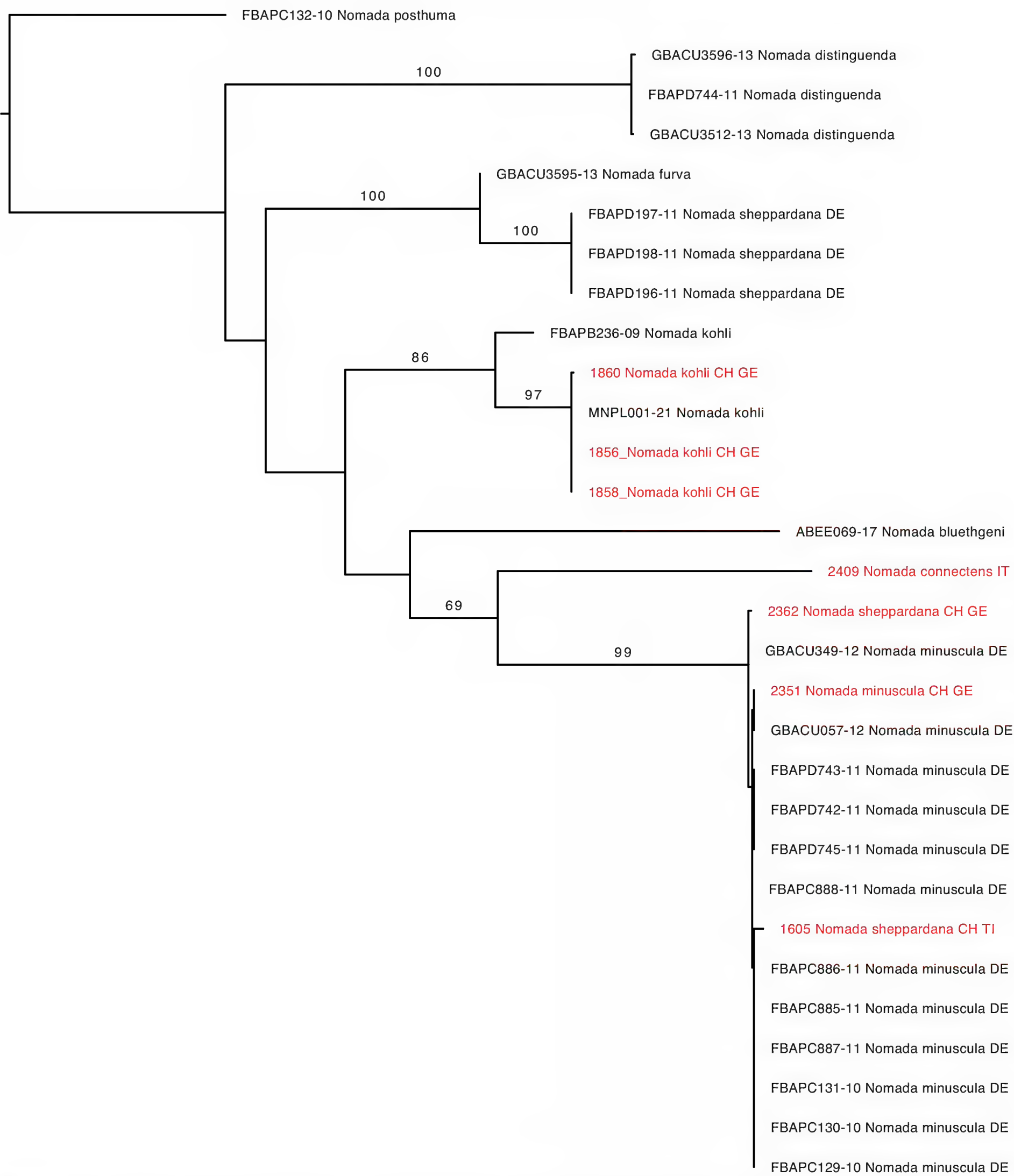
### *Pseudoanthidium nanum* (Mocsáry, 1880)

The central European taxon present in Switzerland is *Pseudoanthidium nanum*, whereas *P. scapulare* (Latreille, 1809) is a western Mediterranean species absent from Switzerland (Litman et al. 2021).

### *Sphecodes alternatus* Smith, 1853

Two mentions from the Swiss Plateau and in Graubünden (Amiet et al. 2014) were based on misidentified specimens. In Switzerland, the species is known so far only from Ticino, as well as from historical records near Geneva.





**Figure 7.** Phylogenetic tree based on maximum likelihood analyses of the mitochondrial gene Cytochrome Oxidase I for individuals of *Nomada minuscula*, *N. sheppardana* and closely related species. Values above branches indicate bootstrap support values based on 1000 bootstrap replicates (values below 50 are omitted). The tree was rooted on the branch leading to *Nomada posthuma*. The two-letter code after the species name indicates the country where the specimen was collected; for specimens collected in Switzerland, the canton is also given as a two-letter code (see caption to Table 2).

***Sphecodes crassanus* Warncke, 1992**

This species is known from two males from Switzerland, one collected in the Valais in 1928, another from Peney in 1884. The date of the record from Peney (5 May 1884)

is dubious, but the record from the Valais originates from a reliable collection and is accepted here. The species occurs locally in northern Italy (Val d'Aosta, Val di Susa) in habitats highly similar to those found in the Valais, rendering the Swiss occurrence plausible.



***Sphecodes cristatus* von Hagens, 1882**

Several mentions from the Swiss Plateau (Amiet et al. 2014) were based on misidentified specimens. In Switzerland, known occurrences of this species are restricted to historical records near Sierre (Valais) and recent records near Basel.

***Sphecodes croaticus* Meyer, 1922**

This species has recently been found in the Valais, where it was probably present but undetected before (Amiet et al. 2014).

***Sphecodes marginatus* von Hagens, 1882**

Most previous records (Amiet et al. 1999, 2014) were based on misidentified female specimens. Known records of this species in Switzerland are restricted to historical records (based on males) in the Geneva region.

***Sphecodes zangherii* Noskiewicz, 1931**

The mention from the Geneva region (Amiet et al. 2014) was based on a misidentified specimen. The species occurs locally in the Valais and has recently been detected in Ticino.

***Stelis minima* Schenck, 1861 and *Stelis minuta* Lepeletier & Audinet-Serville, 1825**

The status of these two taxa is controversial (Schmidt et al. 2015); our DNA barcoding data (Suppl. material 5) confirm that both taxa share DNA barcodes (Schmidt et al. 2015). For now, we continue to recognize them as separate species awaiting additional investigations.

***Stelis simillima* Morawitz, 1876**

This species was first mentioned for Switzerland by Kouakou et al. (2008) in Ticino and has since then been reported from several sites in this canton.

***Tetralonia malvae* (Rossi, 1790)**

*Tetralonia macroglossa* (Illiger, 1806) is treated as a synonym of *Tetralonia malvae*, following Michener (1997). By contrast, Scheuchl et al. (2023) state that the identity of *Apis malvae* Rossi, 1790 is unclear since the original description could apply to other eucerine species, for example *T. nana* (Morawitz, 1874). Regardless of the interpretation of this name, another name would have priority over *T. macroglossa* for this taxon: *Eucera antennata* Fabricius, 1793, for which a neotype was designated (Michener 1997). *Eucera antennata* is the type species of the genus *Tetralonia* and thus, in our opinion, can not simply be called a *nomen dubium* or a *nomen oblitum*, since such an approach would threaten taxonomic stability by ren-

dering the identity of the genus *Tetralonia* unclear (see also comments under *Halictus eurygnathus*, above). The best approach to minimize nomenclatural changes would be to designate a neotype for *Apis malvae*, corresponding to the current concept of this species. Awaiting this, we keep the name *T. malvae* and treat *T. macroglossa* as a junior synonym.

This species, previously considered to be extinct in Switzerland (Amiet 1994), was observed in several sites near Geneva in 2019 and after, suggesting a recent range expansion from France after local extinction.

***Tetralonia pollinosa* (Lepeletier, 1841)**

This species is known from a single specimen collected in Sierre by Frey-Gessner. Since Frey-Gessner's collection is reliable, this record is accepted (see also comments under *Amegilla salviae*).

***Triepeolus tristis* (Smith, 1854)**

This species was recently observed in Ticino in association with *Tetralonia dentata* (Germar, 1839) (Bénon and Giollo 2022).

**Species excluded from Switzerland*****Andrena anthrisci* Blüthgen, 1925**

This species was previously treated as a native species in Switzerland (Amiet et al. 2010). Identification in this group is challenging, and the separation of *Andrena anthrisci* from *A. semilaevis* Pérez, 1903 particularly difficult (Schwenninger 2009; Wood 2023a). We present DNA barcodes for three specimens originating from Germany and identified as *A. anthrisci* by H. Schwenninger (Suppl. material 5). These specimens had identical barcodes with *A. minutuloides* Perkins, 1914. Given that the separation of these two species based on morphology is straight-forward due to the absence of a gradulus at the base of the terga in *A. anthrisci*, this result probably highlights a case of mitochondrial introgression between distinct species, *A. minutuloides* and *A. anthrisci*, in Europe. By contrast all barcoded specimens of *A. semilaevis* in Switzerland (Suppl. material 5) and Germany (Schmidt et al. 2015) had a distinct DNA barcode.

We barcoded several Alpine specimens initially identified as *A. anthrisci* using the key of Amiet et al. (2010). The female specimens had identical DNA barcodes with *A. semilaevis*; although their tergal margins were as shagreened as in *A. anthrisci*, the vestiture was longer than typically observed in that species, and we now consider these female specimens to be atypical, strongly shagreened specimens of *A. semilaevis*. The male specimens had identical DNA barcodes with *A. minutuloides*; while DNA barcodes do not allow for a separation of *A. minutuloides* and *A. anthrisci*, we consider these specimens to



belong to *A. minutuloides* due to the presence of a gradulus at the base of the terga.

These identifications, as well as the identification of older specimens, which could not be analysed genetically, remain tentative. Most of us therefore prefer to exclude *A. anthrisci* from the Swiss fauna. One of us (MH) however considers *A. anthrisci* to occur in Switzerland based on specimens identified using morphology; these specimens could not be analysed genetically.

#### ***Andrena hystrix* Schmiedeknecht, 1883**

This species is mentioned in southern Switzerland by Stöckhert *in* Schmiedeknecht (1930). The presence of this species in Switzerland is highly possible given its wide historical distribution in France (Warncke et al. 1974). However, we exclude it from the Swiss checklist since we were not able to find specimens to back up this record.

#### ***Andrena nigriceps* (Kirby, 1802)**

This species was previously mentioned for Switzerland based on a single specimen collected in the Valais (Amiet et al. 2010). This specimen turned out to belong to *Andrena freygessneri* Alfken, 1904 after examination, and thus *A. nigriceps* is removed from the Swiss checklist.

#### ***Andrena stabiana* Morice, 1899**

Pérez (1903) described *A. emarginata* Pérez, 1903 from “Marseille, Suisse, Majorque, Sicile”; the lectotype is a male labelled “Suisse”, with no further indication on the locality. This taxon is treated as a synonym of *A. stabiana* (Gusenleitner and Schwarz 2002), a placement confirmed by Schwenninger (2007) based on the examination of the lectotype. The historical presence of *A. stabiana* in southern Switzerland is possible given the distribution of this species in northern Italy. However, given the vague locality information of the lectotype of *A. emarginata*, this species is not included in the Swiss checklist.

#### ***Andrena ventricosa* Dours, 1873**

A single male of this species is preserved in the Tournier collection. It is labeled “P. [Peney], 12.07.1890”. Given that this record is based on a single male, that the date (for a fresh male specimen) is somehow unlikely (though not impossible), and that this species with a conspicuous morphology is not mentioned by Frey-Gessner (1899–1916), we exclude this species from the Swiss checklist. We stress that its historical presence in the Geneva region is, however, not impossible in the light of the European distribution of this species.

#### ***Camptopoeum friesei* Mocsáry 1894**

This species was mentioned as resident in Switzerland by Reverté et al. (in press), for unclear reasons.

#### ***Colletes nasutus* Smith, 1853**

There is only a single male of this species recorded for Switzerland (Peney, 4.6.1886, leg. & coll. Tournier). Since this record is far outside the known range of *Colletes nasutus* (closest record in Eastern Germany), this species is excluded from the Swiss fauna. We stress that its presence in Switzerland at the end of the 19<sup>th</sup> century in habitats that are now completely transformed is not impossible. However, following the general guidelines applied for this checklist, we do not include this species in the Swiss checklist.

#### ***Hylaeus lineolatus* (Schenck, 1861)**

This species was mentioned as resident in Switzerland by Scheuchl and Willner (2016) and by Reverté et al. (in press), for unclear reasons.

#### ***Lasioglossum sphecodimorphum* (Vachal, 1892)**

A single female of this species is known from Switzerland (Peney, 15.6.1884, leg. & coll. Tournier). Since this record is far outside the known range of *Lasioglossum sphecodimorphum*, this species is excluded from the Swiss checklist.

#### ***Nomada basalis* Herrich-Schäffer, 1839**

The only record of this species in Switzerland is based on a specimen deposited in the Tournier collection; the specimen is only labelled “Genève”, with no date, unlike most other bees collected by Tournier. Given that the collector is not specified and that only very few bees at that time were labelled with this vague locality (most bees from the Geneva region and from that time were labelled with more precise neighbourhoods or villages such as “Champel” or “Carouge”), this record is not accepted, and *Nomada basalis* is excluded from the Swiss fauna.

#### ***Nomada gribodoi* Schmiedeknecht, 1882**

A single record is available for this species in Switzerland, a specimen supposedly collected near Basel by W. Schmid, without further indication. Since *N. gribodoi* is unknown in Germany near Basel despite intensive collecting efforts, we consider this record as dubious and remove the species from the Swiss checklist.

#### ***Nomioides facilis* Smith, 1853**

This species was mentioned as resident in Switzerland by Reverté et al. (in press), for unclear reasons.

#### ***Nomioides minutissimus* (Rossi, 1790)**

This species was mentioned as resident in Switzerland by Scheuchl and Willner (2016), for unclear reasons.



### *Pseudoanthidium scapulare* (Latreille, 1809)

This species was mentioned as resident in Switzerland by Reverté et al. (in press), probably based on confusions with *Pseudoanthidium nanum*; see under that species.

## Discussion

About 2130 bee species occur in Europe (Ghisbain et al. 2023; Reverté et al. in press). Within Europe, the highest bee diversity is found in the Mediterranean countries, such as Greece, Spain and Italy hosting about 1190, 1170 and 1050 species, respectively (Reverté et al. in press). Based on the present checklist, 632 bee species (including the honeybee *Apis mellifera* and the exotic species *Megachile sculpturalis*) have been recorded for Switzerland to date, which accounts for 30% of the European bee diversity. However, almost 10% of these Swiss species are regionally extinct (Müller and Praz, in press), resulting in 575 species currently occurring in Switzerland and reducing the proportion of the Swiss bee fauna to 25% of the European fauna. The number of bee species found in Switzerland today is distinctly less than the 680 and 975 species assumed to be actually present in Austria and France, respectively, but almost identical to the 570 bee species currently occurring in Germany (Reverté et al. in press; see also Scheuchl 2023), a country that is almost nine times as large as Switzerland. Given the small size of the country, the Swiss bee fauna is remarkably rich compared to all the more northern countries of Europe including Germany.

### Pattern of bee diversity in Switzerland

The remarkable richness in bee species in Switzerland can be explained by the habitat and climatic heterogeneity created by the two main mountain ranges that cross Switzerland, the Jura and especially the Alps. These two mountain ranges divide the country into several biogeographic regions (Gonseth and Sartori 2022), each characterized by strikingly different climatic conditions.

The southern flanks of the Alps are parts of the Po and Adige watersheds; these southern valleys are characterized by insubric climatic conditions with relatively mild winters and wet summers, and are densely covered with thermophilic deciduous forests such as oak (*Quercus* sp.), European hop-hornbeam (*Ostrya carpinifolia* Scop.) or chestnut (*Castanea sativa* Mill.). The southern flanks of the Alps host several remarkable bee species, such as *Tetralonia inulae* Tkalců, 1979 or *Andrena namula*, both of which are rare in central Europe. In addition, numerous Mediterranean species reach their northern distribution limit in Ticino, for example *Andrena pellucens*, *Ceratina chalcites* Germar, 1839, *Tripeolus tristis*, *Andrena livens* Pérez, 1895 or *Nomada carnifex* Mocsáry, 1883 (the two

latter are now considered extinct in Switzerland; Müller and Praz, in press).

By contrast, the northern flanks of the Alps, as well as the Jura, are characterized by high rainfall and cold winters and are mostly covered with coniferous forest that are dominated by European spruce (*Picea abies* (L.) H. Karst.) and European silver fir (*Abies alba* Mill.). These areas overall exhibit a lower species diversity, but host numerous boreo-alpine species, whose distribution becomes sparser from north to south in Europe; examples include *Osmia nigriventris* (Zetterstedt, 1838) (Müller et al. 2019), as well as *Andrena coitana* (Kirby, 1802) and its cuckoo *Nomada obtusifrons* Nylander, 1848 or *Andrena tarsata* and its cuckoo *Nomada tormentillae*. The Alps host only two strict Alpine endemics: *Osmia steinmanni* Müller, 2002 and potentially *Panurginus sericatus* (although see taxonomic notes above on the status of the latter taxon), a low proportion compared to other insect groups, such as butterflies or grasshoppers. Most alpine bee species present in the Swiss Alps also occur in other mountain ranges, e.g., in Western Europe (Pyrenees or Iberian Peninsula, e.g. *Andrena allosa*, *Bombus gerstaeckeri* Morawitz, 1881, *Bombus inexpectatus*, *Bombus mendax*, *Hylaeus glacialis*); in the Apennines or the Balkans (e.g. *Andrena amieti*, *Lasioglossum alpigenum*, *Andrena montana*); or they occur in Scandinavia (e.g. *Bombus alpinus* (Linnaeus, 1758)).

The highest peaks of the Jura mountains, mostly located in its western parts near Geneva, also host several alpine or boreo-alpine species, such as *Anthidium montanum* Morawitz, 1865, *Bombus mesomelas*, *B. mucidus*, *B. sichelii* Radoszkowski, 1859 and, historically, *B. mendax*, *B. monticola* Smith, 1849 and *B. pyrenaeus* Pérez, 1879. This part of the Jura hosts the southernmost population of *B. distinguendus* in Europe (Bénon et al. 2020), a species absent from the Alps.

The most distinctive and entomologically rich Alpine regions are the inner alpine valleys (Fig. 8), characterized by a much drier climate due to the rain shadow effect caused by the surrounding high mountains; see Steinmann (2002) for a summary of the bees associated with these inner alpine valleys, and Braun-Blanquet (1961), Delarzes et al. (2015), and Dengler et al. (2020) for a botanical description of the xeric grasslands and steppes that typically cover the south-facing slopes of these inner valleys. This rain shadow effect results in submediterranean, slightly continental climates with cold winters and dry and hot summers. Habitats in these inner alpine valleys offer isolated northern outposts in Central Europe for numerous Mediterranean species, for example *Ameigilla albigena* (Lepeletier, 1841), *Anthophora mucida* Kriechbaumer, 1873, *Colletes sierrensis* Frey-Gessner, 1903, *Dasypoda argentata* Panzer, 1809, *Epeolus productulus* Bischoff, 1930, *Hoplitis praestans* (Morawitz, 1893), *Lasioglossum elegans* (Lepeletier, 1841), *Melecta festiva* Lieftinck, 1980, *Melitturga clavicornis* (Latreille, 1806), *Nomada mutabilis*, *Osmia anceyi* Pérez, 1879, *Pasites maculatus*, *Protosmia minutula* (Pérez, 1896),





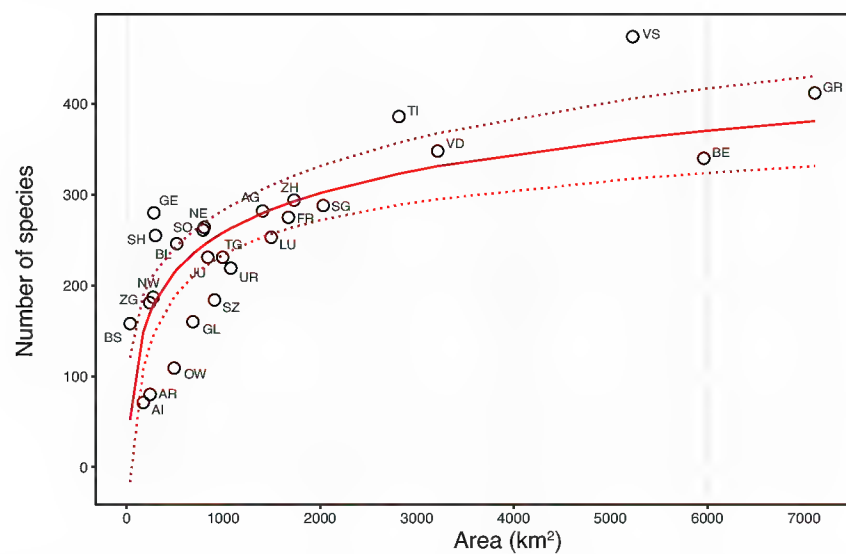
**Figure 8.** Steppic grasslands characterizing the dry, inner Alpine valleys of Switzerland. These habitats represent important bee hot spots in Switzerland and in Central Europe. **A.** Mosaic of xeric grasslands, *Juniperus* steppe (in the background), and cultivated, extensive grassland (on the right) in Zeneggen, Valais; the yellow flower on the left is *Erysimum rhaeticum* (Hornem.) DC, the main or exclusive host plant of *Andrena probata* in Switzerland; in this 756-hectare municipality 307 species of bees have been recorded since 1943 (233 species in the last 20 years); **B.** Steppic grassland near Erschmatt, Valais; **C.** Flower-rich, extensive grassland near Scheidd, Graubünden; **D.** Steppic grassland near Ortenstein, Graubünden. Picture by Christophe Praz (**A**) and Albert Krebs (**B–D**).

*Sphecodes dusmeti* Blüthgen, 1924, or *Thyreus hirtus* (de Beaumont, 1940). Many of these species are also present in other alpine inner valleys in France or in Italy such as the Valle d'Aosta or the Val Venosta (Steinmann 2002), but are otherwise restricted to the Mediterranean parts of southern Europe. These inner-alpine, steppic habitats harbor 42 species which currently do not occur elsewhere in Switzerland, and host populations of species that are widely distributed, but overall rare and isolated in Europe, such as *Andrena simillima* Smith, 1851, *Lasioglossum laeve* (Kirby, 1802), *L. elegans*, and historically *Andrena assimilis*, *A. fuscata*, *A. hypopolia* Schmiedeknecht, 1884, and *A. incisa*. Lastly, the most distinctive elements of these alpine inner valleys are some species with a

strongly disjunct distribution in the Western Palearctic, i.e., *Andrena probata*, which is known only from the upper Valais, Italy, Albania, North Macedonia, Greece and Turkey, and *A. ranunculorum*, which occurs in a few isolated populations between the Pyrenees and the Caucasus including the upper Valais (Gusenleitner and Schwarz 2002). Numerous other insect species present in the upper Valais exhibit similar disjunct distributions, such as the rare butterfly *Kretania trappi* (Verity, 1927).

This increased diversity in regions harboring inner valleys with dry climates is also apparent when considering the diversity in the different cantons (Table 2 and Suppl. material 4; Fig. 9). In terms of number of species recorded after 1999, the cantons of Valais (n = 475 species) and





**Figure 9.** Relationship between the area of the 26 Swiss cantons (in km<sup>2</sup>) and the number of bee species recorded in each canton after 1999. The red line indicates a linear model between the area and the logarithm of the number of species (see text for details), the dotted lines represent the 95% confidence interval. See caption to Table 2 for the canton abbreviations.

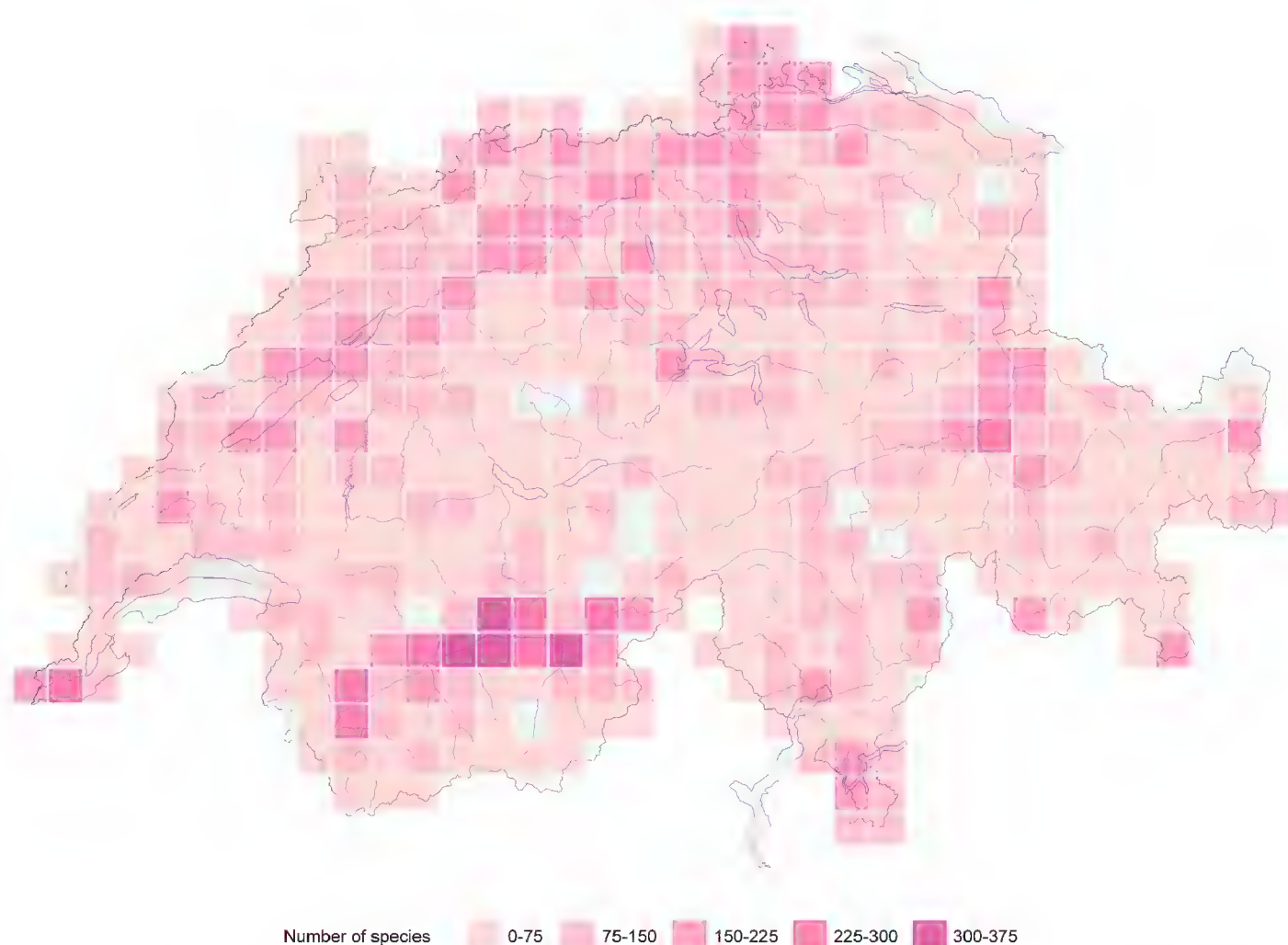
Graubünden (413 species) rank first followed by Ticino (387 species), Vaud (348 species) and Berne (341 species) (Table 2 and Suppl. material 4). These five cantons are also the largest, suggesting that bee species diversity is largely determined by surface area. In fact, there is a significant positive relationship between the number of bee species and the area of the canton (linear model between the area and log (number of species),  $F=39.99$ ,  $df = 24$ ,  $p < 0.001$ ,  $R^2=0.625$ ; Fig. 9).

The two cantons with large dry, inner valleys (VS and GR) had substantially more species than the large canton of Bern, which is characterized by a more humid climate typical of the northern flank of the Alps (Fig. 9).

Similarly, other cantons located along the northern flanks of the Alps (SZ, GL, OW, AI, AR) were also those with comparatively low species diversity (Fig. 9). Although also with a more humid climate, the Ticino canton is characterized by high species diversity; the numerous submediterranean species inhabiting the southern parts of the canton probably explain this high species richness.

The Valais and Graubünden also rank among the most bee species-rich cantons of Switzerland in terms of regional and local diversity. Nine of the ten most diverse 10×10 km<sup>2</sup> squares across Switzerland are located in these two cantons, comprising 237–357 species recorded after 1999, clearly indicating that these regions harbour nationwide hotspots of bee diversity (Fig. 10). These hotspots lie in the xeric inner valleys of the Valais (around Martigny and between Sion and Visp) and Graubünden (Domleschg to Chur) cantons as well as southwest of Geneva.

The inner alpine valleys of the Valais and Graubünden cantons are not only hotspots of bee diversity in Switzerland containing a large number of rare and exclusive species, but are also very rich in species on a larger geographical scale. The results of recent modelling of the taxonomic bee diversity across Europe revealed that the inner alpine valleys of Switzerland harbour particularly diverse bee communities on a continental scale (see fig. 1i in Leclercq et al. 2023), rendering them of European importance. In fact, probably the most species-rich bee fauna of central Europe was identified around Erschmatt in the Valais, where 247 bee species were recorded and 280 species statistically estimated on an area of just 2 km<sup>2</sup> (Oertli et al. 2005). Likewise, in the municipality of Zeneggen (Fig. 8A), with an area of just over 7 km<sup>2</sup>, 307 species of bees have been recorded since 1943 (233 species in the last 20 years).



**Figure 10.** Map of Switzerland with a grid of 10 × 10 km; the colors reflect the number of bee species detected after 1999. The bee diversity hotspots of the Valais and Graubünden cantons are visible.



## Conclusions

With 632 species ever recorded and 575 species assumed to currently occur, Switzerland hosts a remarkably rich bee fauna given the country's small size.

This high diversity is largely due to i. the pronounced topographic and climatic heterogeneity, which allows the occurrence of both highly thermophilous and strictly cold-adapted species within the country's borders, and ii. the geographic connection to Italy and France via the southern flanks of the Alps and Geneva, which act as immigration routes for species from more southern regions. The importance of these immigration routes is clearly evident from the fact that since 2000 about 20 bee species, either previously unknown for Switzerland or which had disappeared from the country for several decades, have colonized areas close to the borders of Italy and France, most likely due to climate warming (Müller and Praz, in press). Within Switzerland, the inner alpine valleys of the Valais and Graubünden cantons are hotspots of bee diversity due to the particularly diverse bee communities containing many rare and endangered species, the presence of numerous species not found elsewhere in Switzerland and the occurrence of isolated populations of species having widely disjunct distribution areas across the Western Palearctic. As the inner alpine valleys are not only of Swiss but even of European importance in terms of taxonomic bee diversity, appropriate measures must be taken to maintain and promote this exceptionally high diversity of bees.

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## Supplementary material 1

### Locality labels from important historical bee collections in Switzerland

Authors: Christophe Praz, Andreas Müller, Dimitri Bénon, Mike Herrmann, Rainer Neumeyer

Data type: tif

Explanation note: **fig. S1: A.** Original, hand-written label by E. Frey-Gessner (Genthod, 20.vi). **B.** Original, printed and hand-written label by E. Frey-Gessner (Genthod, 5.v). **C.** Recopied label from the collection E. Frey-Gessner, associated with a specimen of *Epeolus alpinus* supposedly collected in Genthod near Genève; this (in Switzerland) alpine species is probably absent from the Geneva Region. **D.** Original label by M. Paul (Sierre, 29.v.[18]85). **E.** Printed label from the Chevrier Collection; the hand-writing, presumably from E. Frey-Gessner, has likely been added after Chevrier's death. **F.** Printed label from the W. Schmidt collection. **G.** Original label from the H. Tournier Collection (P[eney]. 27.vi.[18]89); **H.** Original label from the Jabob Collection (Serroux [Le Landeron, Serroux], 1.ix.[19]05); **I.** Original label from the T. Steck Collection (Wallis, Useigne [Euseigne], 21.vi.1925).

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Link: <https://doi.org/10.3897/alpento.7.112514.suppl1>



## Supplementary material 2

### Primers used to amplify and sequence the mitochondrial gene Cytochrome oxidase I

Authors: Christophe Praz, Andreas Müller, Dimitri Bénon, Mike Herrmann, Rainer Neumeyer

Data type: xlsx

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Link: <https://doi.org/10.3897/alpento.7.112514.suppl2>

## Supplementary material 3

### Locality, collection data and BOLD accession numbers for specimens sequenced in this study

Authors: Christophe Praz, Andreas Müller, Dimitri Bénon, Mike Herrmann, Rainer Neumeyer

Data type: xlsx

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## Supplementary material 4

### Checklist of the Swiss bees and presence of each species in each canton

Authors: Christophe Praz, Andreas Müller, Dimitri Bénon, Mike Herrmann, Rainer Neumeyer

Data type: xlsx

Explanation note: Open circles indicate records before 2000, closed circles after 1999. Abbreviations: AG: Aargau; AI: Appenzell Innerrhoden; AR: Appenzell Ausserrhoden; BE: Bern; BL: Basel-Landschaft; BS: Basel-Stadt; FR: Fribourg; GE: Geneva; GL: Glarus; GR: Graubünden; JU: Jura; LU: Luzern; NE: Neuchâtel; NW: Nidwalden; OW: Obwalden; SG: St. Gallen; SH: Schaffhausen; SO: Solothurn; SZ: Schwyz; TG: Thurgau; TI: Ticino; UR: Uri; VD: Vaud; VS: Valais; ZG: Zug.

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Link: <https://doi.org/10.3897/alpento.7.112514.suppl4>

## Supplementary material 5

### Distance-based tree

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Data type: pdf

Explanation note: Distance-based tree build using the unweighted pair group method with arithmetic mean (UPGMA) based of the mitochondrial gene Cytochrome Oxidase I for all individuals sequenced in this project. Previously published sequences (Praz et al. 2019, 2022; Gueuning et al. 2020, McLaughlin et al. 2023) are also included.

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